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VOLUME 10 JUNE, 1934 SPECIAL NUMBER

THE BEECH BARK DISEASE

A *NECTRIA* DISEASE OF *FAGUS*, FOLLOWING *CRYPTOCOCCUS FAGI* (BAER.)[1]

BY JOHN EHRLICH[2]

Abstract

This paper is concerned with a disease of beech *(Fagus)* caused by the sequent activity of a scale insect and a parasitic ascomycetous fungus. Although the writer's studies have dealt almost exclusively with the American beech *(F. grandifolia* Ehrh.), the insect has been observed on *F. grandifolia* var. *caroliniana* Fern. and Rehd., as well as on the European beech *(F. sylvatica* L.) and a number of its varieties. The name "beech bark disease" is proposed.

The European history of this disease, gleaned largely from the literature on the insect, is reviewed, beginning with the first reports of injury at the middle of the last century in England and Germany, tracing its reported activity to the present, and the conclusion is reached that the disease is not now regarded as so serious an affliction of beech as formerly and that it is widespread and enphytotic in central and western Europe. In America the disease has been active for approximately 15 years; it first attracted attention in the vicinity of Halifax, Nova Scotia, and has spread steadily until it is now active throughout Nova Scotia, in southern New Brunswick, and in localized areas of eastern and south central Maine, although the insect pathogen has been present also for perhaps a decade in eastern Massachusetts. A pathological line-plot cruise of typical affected areas in Nova Scotia and New Brunswick demonstrated that, in the stands examined, the beech infected by the fungus had attained a uniform mean of 90% and that in the regions infested for a longer period approximately 50% of the beech had been killed at the time of observation. The conclusion is reached that the disease in America is assuming the proportions of a fatal and spreading epiphytotic.

The first indications of the disease are the appearance of the minute insect on the bark of trunk and branches, and the subsequent development of fruiting bodies of the fungus in the areas previously occupied by the insect. The insect probes the living tissues of the outer bark, extracting protoplasmic materials and causing the death of punctured cells. The shrinkage of groups of killed cells leads to tearing of the periderm, which enables the fungus to initiate infection. Once past the barrier of phellem, the fungus is able to advance through

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Toward the cost of publication of this paper the Arnold Arboretum has made a substantial contribution.

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the living tissues of bark, cortex, phloem, cambium, and sapwood. Death of the infected tissues interferes with normal conduction and storage in the trunk and results in a progressive killing of the tree, which becomes complete when the fungal lesions have coalesced sufficiently to effect an interruption in conduction. As infestation progresses, the foliage and twigs dry and die, whole branches cease to leaf out, and large areas of bark on the trunk crack, usually loosen from the wood, and eventually fall away. On younger trees infection is less abundant, the fungus advances less readily, and individual lesions frequently become surrounded by healthy bark and wood, and eventually form depressed areas but never typical scalariform cankers.

The insect (*Cryptococcus fagi* [Baerensprung]) which initiates this disease has been reported from Germany, Switzerland, Czechoslovakia, France, Belgium, Holland, Sweden, the British Isles, eastern Canada (where it was first reported in 1914 and has probably been present since 1890), and the northeastern United States (where it was discovered by the present writer in 1929). Synonymy, previous descriptions of the insect (a member of the Homopterous family Coccidae), and its life history are reviewed, with personal notes on habits, dissemination and long range distribution, and factors influencing infestation.

The fungus following the insect in America is a species of *Nectria* in the *coccinea* group as defined by Wollenweber. Its specific identification must await a thorough comparative study of the American forms, but spore measurements indicate that it is an undescribed variety of *Nectria coccinea* (Pers.) Fries. A brief description is given. The fungus has been repeatedly isolated and grown in pure culture on a variety of media, producing conidia and ascospores. The influence of low temperature, aeration, and hydrogen ion concentration are discussed and data given on the height of ascospore discharge. Spore-trap experiments demonstrated that ascospore discharge follows rains of sufficient duration to wet the bark and continues until after the surface of bark and perithecia appears dry; both ascospores and macroconidia are air borne.

The role of each of the pathogens in producing the disease has been demonstrated. The evidence consists of the following: (1) the constant association of the organisms with the disease, (2) absence of the disease when one only is present, (3) consistent isolation of the fungus from infected tissues, and (4) the inability of the fungus to infect tissues not infested by the insect and its ability to infect those infested. The insect probes the bark, resulting in a rupture of the periderm attendant on death and shrinkage of the living cells of the bark on which the insect feeds. This enables initial infection by the fungus. The fungus grows parasitically, causing the death and destruction of the storage and vascular systems of the trunk and branches.

The fungus is shown by experiments to be able in general to enter and infect extensively only bark on which the insect has been present for approximately a year or longer. Observations in each of three consecutive years on tagged trees in permanent sample plots show that, once the trees become generally infested by *Cryptococcus fagi*, *Nectria* infection develops on the majority within three years and kills some of them in one or two years. Later, almost the entire stand becomes infected and the amount of infection builds up rapidly, with resulting mortality.

A pathological line-plot cruise of 200 plots containing 4,483 beech shows on analysis small but definite positive correlation between percentage of beech infected by *Nectria*, and percentage of beech in stand, position on ridge, and steepness of slope; severity of infection shows definite correlation with diameter (d.b.h.),* and questionable correlation with forest type, and crown density. Mortality, expressed as percentage of beech (over 3 in. d.b.h.) killed, is correlated with diameter, crown class, and position on ridge, and questionably with forest type, and steepness of slope.

The disease can be controlled on ornamental trees by early eradication of the insect with insecticides. Control in forest stands should aim first at the salvage of infected, dying, and recently killed timber, for the purposes of obtaining the greatest possible return on a rapidly depreciating investment and of preventing the development in the slash of unsanitary conditions conducive to further deterioration in the remaining stand. Second, control should aim at the possibility of combatting the insect pathogen with fungal and insect enemies. Third, it should, by forest management, favor beech on broad ridge tops rather than steep slopes, and cull the larger trees in an attempt to produce changes in the environment designed to restrict activity of the pathogens and substitute a younger, less susceptible stand.

**Diameter at breast height.*

I. Introduction

The subject of the investigation reported in the following pages is a disease of beech (*Fagus*), new to America. Its rapid and destructive spread has created the task of determining its cause and its *modus operandi*, and from the knowledge obtained with respect to these features the obligation of endeavoring to formulate a technically sound and economically feasible program of control. Underlying problems in both directions, as well as related ones, have been investigated and are discussed in this paper.

Associated with the disease are the attacks of an insect, a minute coccid conspicuous by reason of its woolly, white, wax secretion. This has been the topic of many entomological studies and observations, especially in Europe. The present research has disclosed the fact, however, that the insect merely paves the way for a fungus which is responsible for most of the injury and ultimate death of the beech. This fact has necessitated a change of viewpoint; the emphasis is here directed to a disease of a forest and shade tree, rather than to an insect pest or fungi associated with it.

II. Suscepts

The disease is known on the two western species of beech only: the European (*Fagus sylvatica* L.) and the American (*Fagus grandifolia* Ehrh.). Although the disease is common on these two species, certain of their varieties are infested to a greater or less extent by the insect. Thus in Great Britain the varieties with copper-colored or bronze-colored leaves (*F. sylvatica* var. *atropunicea* West., etc.) are reported as more or less attacked by the insect (Gillanders 1908, Green 1915, Forestry Commission 1926) and the weeping beech (probably *F. sylvatica* var. *pendula* Loud.) as relatively resistant (Newstead 1901, Carpenter 1903). In Holland Schenk (1924) described a "bruin" beech scion (*F. sylvatica* var. *atropunicea* West.) as only sparsely infested, while the common beech stock below the graft union harbored a dense mass of the insects. In the Arnold Arboretum, Boston, Massachusetts, the writer has observed light natural infestation by the insect on the dwarfed contorted *F. sylvatica* var. *tortuosa* Pépin and on the southern variety of the American beech (*F. grandifolia* var. *caroliniana* Fern. and Rehd.). This enumeration is in no sense complete since neither in Europe nor in America have artificial infestation experiments been performed.

III. Names

Most of the early observations were made by entomologists and horticulturists who were not accustomed to go beyond the injury caused by an insect or fungal pathogen. Accordingly few names have been applied to the disease itself. The only European designation known to the writer is Rhumbler's (1914a, b, 1915, 1922) "Schleimfluss-Wollaus-Nectria Krankheit." In America the first references to the disease were made by Faull (1930 a, b) who pointed out the importance in Nova Scotia of the "bark disease of beech."

In preliminary accounts of investigations the writer referred to it as the "bark disease of the beech" (Ehrlich 1931) and as the "beech bark disease" (Ehrlich 1932b). The name "beech bark disease" is used in this paper.

IV. History and Range

In Europe

The early history of the disease is necessarily largely the history of references to the insect *(Cryptococcus fagi* [Baer.]) which is its initial cause. A detailed account of this insect is given below in Section VII A. As early as 1849, however, M'Intosh referred to the outbreak as a disease and noted that it had affected the beech for some years. Since 1849 accounts of injury and mortality have appeared in many entomological papers. The only detailed studies of the effects following insect attack and associated fungi are by Hartig (1880), Boodle and Dallimore (1911), and Rhumbler (1914 a, b, 1915, 1922, 1931*). Hartig described the effects of insect feeding on the tissues of bark, phloem, and cambium, and concluded that fungi which follow, such as *Agaricus adiposus* Fr. and *Nectria ditissima* Tul., are entirely secondary and of little importance. Boodle and Dallimore drew the following conclusion from their observations: "While the Coccus is doing very little harm, certain fungoid pests account for a serious amount of injury, which is usually credited to Coccus. On all the dead trees pointed out to us as having been killed by Coccus, we found destructive parasitic fungi present, which alone would account for the death of the trees." (Boodle and Dallimore 1911: p. 341.) The fungi mentioned are *Nectria ditissima* Tul. on the bark of the trunk, and *Melogramma spiniferum* De Not. on the bark of the roots at the base of the trunk. Rhumbler (1914 a, b, 1915) concluded from extended study and observations that the insect alone never causes the death of a beech, but hastens the effects of a preceding slime-flux infection and the subsequent activity of *Nectria ditissima* Tul. Later (Rhumbler 1922) he described three types of slime-flux infection and concluded his observations on the etiology and course of the "Schleimfluss-Wollaus-Nectria" disease by assuming that an unknown agent enables the development of primary slime-flux lesions (S_I, S_{II}) and light infestation by *Cryptococcus fagi* (Baer.); these three agents are held to be mutually helpful and to give rise to the dangerous S_{III} stage which results in killing, aided by other fungi (especially *Polyporus* [*Fomes*] *fomentarius* [Fries] L. ex. Gill. and *Nectria ditissima* Tul.) and by the borers *Lymexylon dermestoides* L. and *Xyloterus domesticus* L.

The absence of the pathological viewpoint in most of the other European accounts makes it hazardous to evaluate the extent and character of the disease abroad; but one cannot escape the conclusion that it is widespread in Europe, following in general, but certainly not completely, the range of *Cryptococcus fagi* (see section VII A below), and that the disease is enphytotic and occasional rather than epiphytotic in nature.

**The present writer learned of this paper too late to permit examination of more than an abstract.*

In North America

In America the situation has been quite the reverse. The first recorded outbreak occurred in Nova Scotia about 1920, some 30 years after the first known appearance of the insect on ornamental European beech in the Halifax Public Gardens, and some five years after its recognition as general in beech stands in the vicinity of Halifax.* Graham (1927) stated that lumber companies operating along the south shore of Nova Scotia reported during the winter of 1925-26 that the beech stands in that part of the province were in danger of being entirely destroyed by this disease. The first published references to the disease were by Faull (1930a, b) who observed its effects in various parts of the province. Countless verbal statements to the writer as well as personal observations beginning in 1930 have made it clear that death, which is now known to result from infection of the insect-infested trees by a species of *Nectria*, has followed *Cryptococcus fagi* in its steady march in all possible directions from Halifax. By 1930 the disease had become so firmly established throughout the Nova Scotia mainland that hardly a beech stand could be found in which there had not already been some mortality, and in the island of Cape Breton symptoms were becoming evident everywhere. The writer has not visited Prince Edward Island and is therefore uncertain whether the fungus has attacked the insect-infested beech in that province; the Dominion Plant Pathologist, stationed at Charlottetown, writes that he has not yet observed infection. Meanwhile in New Brunswick infection could be found in 1930 as far from the interprovincial boundary as the town of Albert and much mortality had already taken place in Westmoreland County. The spread of infection during the next two years was observed by the writer both in Cape Breton and in New Brunswick: by 1932 the disease had already begun to take its toll in Cape Breton and had advanced in New Brunswick at least 20 miles along the shore of the Bay of Fundy, passing the village of Alma in Albert County. Meanwhile, further scouting showed that the insect had already become established at various points over a much larger area involving the whole of southern New Brunswick (including the counties of Westmoreland, Albert, Saint John, Kings, Queens, and Charlotte) and that young spot infections by the *Nectria* already existed in certain of the insect-infested stands.

The proximity and continued encroachment of this veritable epiphytotic in the Maritime Provinces have stimulated a keen lookout in New England, since neither of the pathogens was known to occur south of the international boundary. As early as 1929 infestations of beech were discovered by the writer in eastern Massachusetts (Essex, Middlesex, Suffolk, and Norfolk

**Thus, two woodsmen, George Dickey, chief district forest ranger, Musquodoboit, Halifax Co., N.S.; George Horne, sub-ranger, Enfield, Halifax Co., N.S., well acquainted with the outlying parts of Halifax County, told the writer that beech had begun to die in the Musquodoboit Valley before 1920, and in the vicinity of Enfield by 1923. A lumberman now operating in Yarmouth County stated in a letter and later told the present writer that, "In 1920, after I returned from the war I had a man clear up quite a few beech trees at my home in Halifax County. These trees had died from some cause . . . . I now feel this was the first of the disease that I noticed. The same year the beech in Colchester County began to die and in 1921 I noticed about an acre near Carleton, Yarmouth Co., that was about all dead." (Boutilier, 1929.)*

Counties) and in 1931 members of the United States Bureau of Entomology (Melrose Highlands Laboratory) found the insect in south central Maine (Ehrlich 1932a). Further surveys in Maine by the State Entomologist during 1932 led to the finding of additional insect outbreaks at many points in an area in the south central part of the state involving parts of the counties of Waldo, Lincoln, and Knox, and an older infestation in Washington County (eastern Maine) adjoining the southern New Brunswick infestation in Charlotte County. A careful watch has been kept by the writer for possible *Nectria* infection and the development of the disease in eastern Massachusetts, but as yet none has been discovered. In the autumn of 1932, however, the State Entomologist for the State of Maine informed the present writer that he had just discovered what appeared to be infection by *Nectria* on insect-infested beech in one of the south central Maine localities, and that similar infection had been found more widespread, more advanced, and associated with mortality in the Washington County areas. In November, 1932, the writer visited the infected stand at Liberty (Waldo County, Maine) and determined that both fungus and disease were the same as in the Maritimes (Ehrlich 1933a, b). The known range of the insect and of the fungus associated with the disease have been indicated on a sketch map (Fig. 1). It will be observed that both are still limited to the maritime margin of the continent; whether this is due merely to the chance origin of the infestation by the sea or to ecological factors which may limit westward distribution can not yet be asserted.

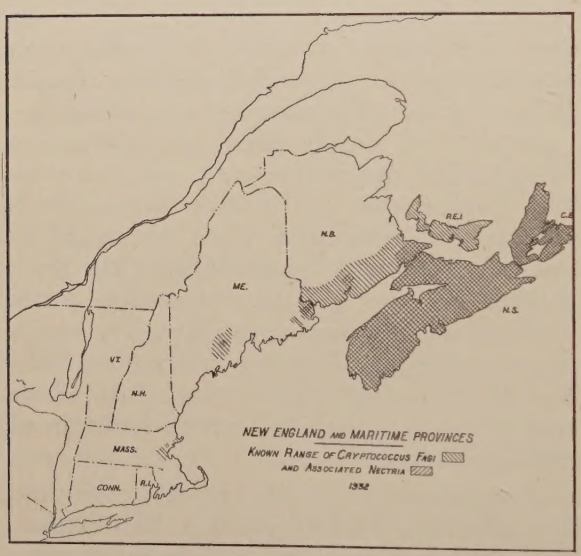

FIG. 1. *Known range (1932) of the pathogens of the beech bark disease in the Maritime Provinces and New England.*

Summarizing, the European accounts indicate that pathological complications of attack by *Cryptococcus fagi* are occasional and become serious only in localized areas. In eastern North America on the contrary, a distinctly epiphytotic disease has developed; a large reserve of inoculum has been built up and fungal infection follows in most cases so closely and abundantly on insect attack that death comes quickly. Furthermore, the pathogens are distributed so rapidly that their progress as well as that of the disease can be observed from year to year over large areas. The disease in North America is known to be active in Nova Scotia and in portions of New Brunswick and Maine.

V. Importance

Historical Résumé

In Germany, Hartig (1880) reported occasional killing of infested trees and concluded that considerable damage might result in young stands, especially those on poor soils, but that in older stands the disease became injurious only in individual cases. Altum (1881) reported that much injury was being caused but gave no data. Nüsslin (1905) merely stated that the importance to forestry of the disease following the woolly beech scale was not slight. Bertelsmann (1913a) gave figures for the district of Ziegelroda, in which, 10 years after an infestation had first been observed, the loss in beech killed amounted to approximately 4000 cubic metres in one year and in each of the following two years, 3000; he pointed out the importance of salvaging such timber promptly, since the wood decays—once the tree is dead—in an incredibly short time. Rhumbler, who published extensive observations on the course of the disease, reported that from 15 to 20% of the heavily infested trees are killed (1931). Thus it may be reasonably concluded that in Germany the disease, though common, is not epiphytotic nor of outstanding economic importance.

In Holland, injury is regarded as less important than was thought at one time (Anon. 1921). Although it "is not taken seriously by the Belgian foresters" (Anon. 1910 : p. 643), Vayssière stated in 1926 (p. 350) : "J'ai pu constater son importance économique en Belgique où, certaines années, les Hêtres de la forêt de Soigne ont leur tronc entièrement couvert par la sécrétion blanche du *Cryptococcus fagi* qui leur donne un aspect tout à fait caractéristique."

In England, with the realization that a new pest was at hand, much fear was experienced as to its possible injurious effects but no actual estimates of damage were made. In later years, either the insect became less injurious or else earlier fears proved to be ungrounded. Thus as early as 1851, C.C. stated in a horticultural journal that "about six or seven years ago the ornamental Beeches, in many of the gentlemen's grounds in Yorkshire were thus attacked and gradually destroyed . . . . " (C.C. 1850 : p. 11). Foggo (1863) wrote of the "fatal disease of ornamental beech." In 1898 Miss Ormerod quoted a letter from Lord Burton, who referred to " . . . . the infestation which is destroying all the Beech trees in the woods here" (Ormerod 1898 : p. 6); two years later she spoke of the insect associated with the disease as very destructive (Ormerod 1900). Newstead, who is responsible for the best entomological account, reported that in eastern Surrey many of the finest trees were being destroyed (1900); that the insect is one of the most destructive of native coccids (1903); and that it is one of the most destructive pests of beech (1905). Theobald (1905 : p. 137) referred to it as "the most serious forest tree pest we have." Perhaps more important than economic losses is the effect which this unfortunate situation was capable of producing in the Rev. Wilks: "We fear the Beech is doomed all over the country, and that the next generation will only know by pictures and reports how gloriously beautiful

our forest Beeches have been" (Wilks 1901-02 : p. 599). In 1907 the insect was characterized as "one of the most destructive pests against which the arboriculturist has to contend" (Boulger 1907 : p. 276). In 1908 MacDougall reported that *Cryptococcus fagi* continues its destructive work. The same year Webster stated: "It is only of late years that the terrible ravages have been felt severely, and that owners of woodlands have been driven to do everything in their power to combat its injurious effects" (Webster 1908 : p. 257). Gillanders (1908 : p. 234) characterized the insect as "one of the most dreaded pests of the arboriculturist." It might be judged from the foregoing references that the insect and its disease were indeed major calamities in the England of three decades ago. But in 1911 Boodle and Dallimore made a painstaking effort to discover just what the effects of *Cryptococcus fagi* really were and how serious they might be; their conclusions are worthy of note: "That the Coccus has not assumed an epidemic state is apparent everywhere" (Boodle and Dallimore 1911 : p. 341). "That it is doing any serious amount of harm, or that it is likely to do so, is doubtful. In some of the early records the disease appears to have been quite as plentiful as it has been of late years, and to have caused the same uneasiness, but the worst expectations were never realized." (*Ibid:* p. 340.) Apparently this conclusion was justified, for as recently as 1925 we read: "The view that Beech Coccus is a serious enemy of the beech is a prevalent one . . . . That view has no support in fact" (Munro 1925 : p. 284). The following year the same view was expressed by the Forestry Commission (1926). But Boodle and Dallimore added the following, which was repeated in 1925 by Munro: "While the Coccus is doing very little harm, certain fungoid pests account for a serious amount of injury, which is usually credited to Coccus. On all the dead trees pointed out to us as having been killed by Coccus, we found destructive parasitic fungi present, which alone would account for the death of trees. The same fungi kill or injure other kinds of trees on which the Beech Coccus does not occur." (*Ibid :* p. 341.) The two most common parasitic species were stated to be *Nectria ditissima* Tul. and *Melogramma spiniferum* De Not.*

While the enphytotic nature of the disease following *Cryptococcus* attacks in Europe has been reflected in only minor economic importance, in America the recent epiphytotic attack is producing losses of great magnitude and even greater potential importance. As early as 1914 in the first published account of the discovery of the insect here, Braucher warned that "if it once becomes firmly established in our beech woods and thrives as it promises to do, it is impossible to foresee the damage that it may cause" (Braucher 1914 : p. 15). By 1926 Hutchings wrote: "Throughout the central and southern parts of Nova Scotia the trees are reported to be in a very serious condition, and there is considerable apprehension as to the losses it has already brought

**Personal observations and consultations with forest entomologists and pathologists in England during the autumn of 1933 have convinced the writer that Cryptococcus fagi is widespread, that parasitic fungi do not here ordinarily follow infestation by the insect, and that no damage can be attributed to the woolly beech scale or to associated fungi in England. The fungi mentioned by Boodle and Dallimore (1911) have been encountered repeatedly, but only on logs, stumps, and standing trunks which had died from other causes.—Author, Kew, March 1934.*

about, the gradual spreading of the trouble to fresh areas being a source of further anxiety . . . . The trees eventually succumb to the attack." (Hutchings 1926 : p. 116.) In the same year the Minister of Agriculture for Canada reported that "the beeches are dying in considerable numbers throughout the infested area" (Motherwell 1926 : p. 98). When in 1929 Faull made a pathological reconnaissance of the forests of Nova Scotia he was at once impressed by the fact that a virulent disease of fungal origin was active in the insect-infested beech, and decided that this "bark disease of beech" was perhaps one of the two outstanding diseases of hardwoods in the province (Faull 1930a, b). At the same time the Associate Dominion Entomologist in charge of the Division of Forest Insects reported that *Cryptococcus*, associated with certain fungi which apparently follow in its wake, was the cause of very extensive injury (Swaine 1930 : p. 45). As a result of observations throughout Nova Scotia during the summers of 1930 and 1931, the present writer stated: "There is hardly a stand of maturing beech in the province in which the disease can not be found, and in most of them a large portion of the trees are either dying or already dead" (Ehrlich 1932b : p. 43). During the past year the Chief Forester of the province judged that of the volume of standing beech timber, estimated at 304,661,000 cu. ft., the disease had already destroyed approximately 100,000,000 cu. ft., or slightly less than one-third (Schierbeck 1932 : p. 17).

In Eastern Canada

The extensive mortality resulting from this disease and the probability of its continued spread prompted the writer to attempt an evaluation of the actual damage resulting. It was realized that such data might also be of value in securing statistical substantiation of theoretical explanations of the influence of environmental factors on the incidence of infection and mortality, which might form the basis for possible silvicultural control experiments. It was therefore decided to employ a modification of the foresters' line-plot cruise, recording data not only on diameter and crown classes for each species and on pathological conditions for beech, but also on factors possibly influencing the disease, such as forest type, percentage of beech in stand, crown density, aspect, position on slope, percentage of slope, and proximity to sea water.

Five regions were selected, each in a different county (Fig. 2); three of them were in portions of the Nova Scotia mainland known to have been attacked for at least 10 years, and in which it might accordingly be assumed that a certain equilibrium had been reached between the aggressiveness of the pathogens and the limiting influence of an environment changed by the progress and effects of the disease. The other two areas, one in Cape Breton and one in New Brunswick, were selected in regions known to have been attacked within approximately the last four to six years, and in which the damage had not yet attained its maximum, but in which possible differences in the early course of injury could be analyzed. The general procedure in making this survey was the standard one employed in timber-estimating

by the line-plot method. In each region typical beech ridges were selected and laid out in such a manner that a fair sampling of approximately 0.5% of the area could be taken; this was usually done by running parallel compass-courses over the area, taking 0.1-acre sample-plots every 10 chains, offsetting at the end of a course for 20 chains (0.25 mile), and then working back on a new line parallel to the old. The compass man (a trained forester) took

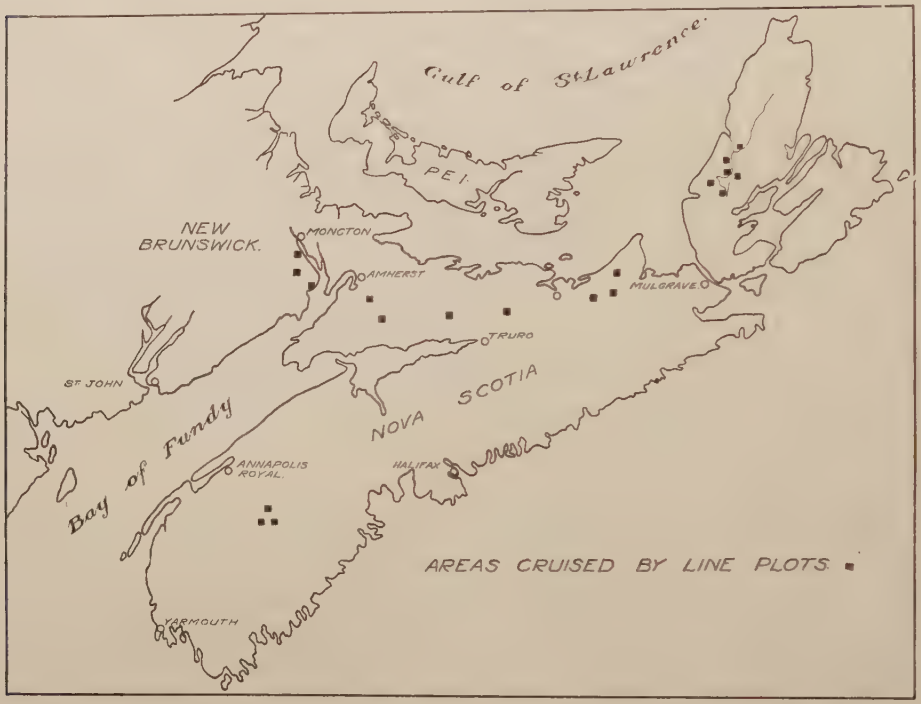

FIG. 2. *Location of areas in Nova Scotia and New Brunswick cruised by line plots.*

preliminary general notes on the plot while the observer ran a measured string around the plot, half a chain to one side of the two-chain tape, two chains parallel to the tape, and half a chain back to the tape, enclosing a plot of one square chain (0.1 acre). The writer made all observations and the compass man recorded the notes on a specially designed form sheet. Each tree was chalked as observed to eliminate the possibility of duplication or omission. The general data on this survey are presented in Table I. It will be observed from the table that a total area of approximately 6.25 square miles (4000 acres) was cruised, in which 200 plots of 0.1 acre each were examined, totalling 20 acres of beech stand in which every tree over three inches in diameter at breast height (4.5 feet) was examined. The total number of trees of all species was 8160, of which 4483 were beech. The mean number of trees of all species per plot was 40.8; of beech, 22.4.

The composition of all line plots by species and diameter classes is shown in Table II. In addition the actual number of beech in each diameter class

TABLE I

GENERAL DATA ON LINE-PLOT SURVEY, 1932

	Nova Scotia mainland	Cape Breton and New Brunswick	Total
Approximate area cruised (in acres)	1,400	2,600	4,000
Approximate percentage of cruised areas examined	0.5	0.5	0.5
Size of individual plots (in acres)	0.1	0.1	0.1
Acreage of all plots	7.0	13.0	20.0
Number of plots examined	70	130	200
Total number of trees (over 3 in. d.b.h.)	2,802	5,358	8,160
Total number of beech (over 3 in. d.b.h.)	1,497	2,986	4,483
Mean number of trees per plot	40.0	41.2	40.8
Mean number of beech per plot	21.4	23.0	22.4

TABLE II

COMPOSITION OF ALL LINE-PLOTS, BY SPECIES AND DIAMETER CLASSES

Genus and species	Per cent of each species in each diameter class						Species totals	
	4–7 in.	8–11 in.	12–15 in.	16–19 in.	20–23 in.	24–27 in.	Number of trees	Per cent of total number of trees
Number of *Fagus* trees	2,506	1,337	519	109	12	—	4,483	—
Fagus grandifolia	55.9	29.8	11.6	2.4	0.3	—	4,483	54.9
Acer saccharum and *A. rubrum*	58.8	25.9	11.0	3.0	0.8	0.4	1,351	16.6
Betula lutea	41.4	28.7	16.9	7.2	5.3	0.5	947	11.6
Abies balsamea	83.7	13.6	2.6	0.1	—	—	821	10.1
Picea rubra and *P. glauca*	65.7	20.4	9.4	4.5	—	—	245	3.0
Tsuga canadensis	56.4	21.8	18.2	3.6	—	—	55	0.7
Betula papyr fera	49.2	30.7	16.6	1.5	2.0	—	199	2.4
Populus grandidentata	38.1	61.9	—	—	—	—	21	0.3
Carpinus caroliniana	100.0	—	—	—	—	—	17	0.2
Quercus rubra	43.8	37.5	18.7	—	—	—	16	0.2
Pinus strobus and *P. resinosa*	40.0	20.0	20.0	20.0	—	—	5	0.1
					Total		8,160	100.1

is given. The table shows that for the plots as a whole the hardwoods, beech *(Fagus grandifolia* Ehrh.), maple *(Acer saccharum* Marsh., *A. rubrum* L.), and yellow birch *(Betula lutea* Michx.), constituted 83.1%, of which 54.9% was beech. The common softwoods constituted only 13.8%, of which fir *(Abies balsamea* Mill.) far outranked spruce *(Picea rubra* Link, *P. glauca* Voss) and hemlock *(Tsuga canadensis* Carr.). The remaining 3.2% consisted of other species.

The most obvious measure of the importance and activity of the disease is the abundance of the pathogens. One measure of abundance is the percentage of the susceptible trees infested by *Cryptococcus* and infected by *Nectria*. Preliminary observations gave convincing evidence that in a diseased stand practically every beech harbors a certain number of the insects, and that, although the rate of increase of the infestation varies, the number ultimately decreases to zero as fungal infection destroys the tissues on which the insect is dependent for food, to the point of killing the tree, so that neither the percentage of beech infested nor the amount of infestation at a given time of observation was judged capable of yielding significant data. Evidence of *Nectria* infection, on the other hand, remains even after death and was judged to afford a more reliable index to the amount of disease which was or had been present.

The percentage of beech in each plot which showed symptoms or signs of *Nectria* infection and the mean or plot percentages for each county were secured. Table III shows the number of sample plots, the total number of

TABLE III

PERCENTAGE OF BEECH INFECTED BY *Nectria* (PLOT-PERCENTAGE MEANS), BY COUNTIES

Regions	Nova Scotia mainland			Cape Breton and New Brunswick		All counties
Counties	Annapolis	Cumberland	Antigonish	Inverness	Albert	
Number of sample plots	29	24	17	100	30	200
Total number of beech in all plots	691	467	339	2,247	739	4,483
Mean plot per cent of beech infected	**92.7** ±1.8*	**87.5** ±1.7	**86.5** ±3.3	**89.4** ±1.4	**90.9** ±1.3	**89.6** ±0.77
Probability odds**	>100 to 1	>100 to 1	>100 to 1	Very great	Much > 100 to 1	Very great

**The figure following the plus-or-minus sign (±) is the standard error of the mean, computed from the individual plot percentages by way of the standard deviation, according to the formula:* $\sigma_m = \frac{\sigma_x}{\sqrt{n}}$, *where* σ_m *is the standard error,* σ_x *is the standard deviation, and n is the number of sample plots.*

***Taking the mean percentage of trees infected as 90%, the values in this row were obtained by computing* χ^2 *from the actual numbers of trees infected in each plot and the numbers expected with a mean percentage infected of 90. The formula employed is:* $\chi^2 = \Sigma\left(\frac{x^2}{m}\right)$, *where x is the difference between the actual and expected number of trees infected, and m is the expected number.*† *Where n (one less than the number of sample plots) was 30 or less, the value of P was read by entering the table of* χ^2 *in Fisher (1930). These probabilities have here been converted into odds. Where n was more than 30, the formula* $\sqrt{2\chi^2} - \sqrt{2n - 1}$ *was employed; when the first term of the formula was less than the second, P was judged to be greater than 0.5.*

The values in this row measure the probability that a sampling (identical with the present one in number of plots and number of beech in each plot), made from a population in which trees were infected at random with a constant probability of infection for each tree (this probability being the 90% actually found), would show deviations as great as, or greater than, those found in the present sampling.

†*See footnote on p. 605.*

beech in all plots, and the mean percentage of beech infected in each county and in all counties combined. The table shows that the mean percentages of beech infected for the various counties range between 86.5 and 92.7, with a mean for all counties of 89.6%, and with small standard errors throughout. These percentages are shown graphically by the vertically ruled bars in Fig. 3. Further, the percentage of infection for each plot is extremely close to the mean for all plots. A measure of this uniformity is given by the probability odds in the table, which show how often random sampling (as defined in the footnote to the table) would give greater deviations from the mean than those found. The odds for each county and for all counties are greater than 100 to 1, which means that the present deviations are exceedingly small; they are, in fact, even less than would be expected by random sampling alone. The reason for this is not clear; it may conceivably be due to bad sampling methods or to fallibility in detecting the lightest infections.† Since the percentage of infection for each plot is so close to the mean for all plots, there is probably no need for further analysis of the data with a view to correlating differences in the percentage of trees infected with possible environmental or other factors. This does not preclude the possibility that sorting the trees in each plot according to size and other characteristics would show significant differences in the percentage of trees infected.

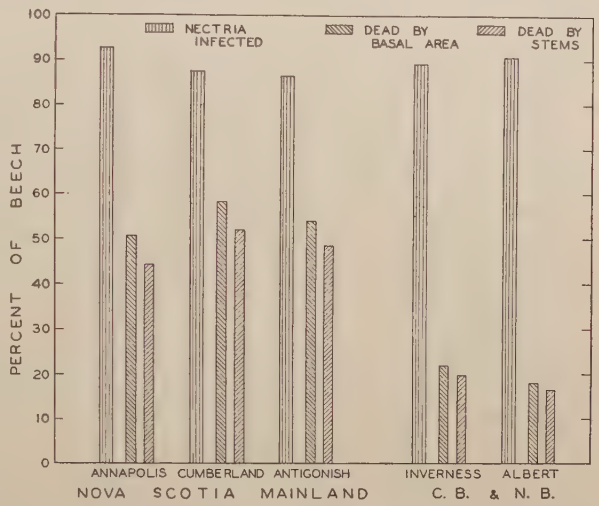

FIG. 3. *Percentages of beech infected by Nectria (according to number of stems), and dead (according to number of stems, and according to basal area), in each of the five counties containing cruise areas.*

It appears from Table III that the areas examined in the five counties do not differ significantly in the percentage of beech infected by *Nectria*, and one might conclude from this that the disease is equally advanced in all. But these figures tell nothing of the severity of the infection on individual trees; that is, they do not distinguish among trees with only scattered or

†*After the completion of the computations, it was realized that* χ^2 *should have been calculated on the basis of the discrepancies of both infected and uninfected trees from expectation, and, instead of the above formula, the method in Fisher (1930: pp. 82-90), section 21, examples 11 and 13, should have been employed. With* χ^2 *increased accordingly by a factor of 10, the values of P obtainable from Fisher's table of* χ^2 *should be decreased materially. The probability odds would be reduced accordingly to more reasonable values, probably indicating that the deviations of individual plot percentages of beech infected by Nectria are not indeed less than would be expected by random sampling alone, but somewhat greater. This opens the possibility that further analysis might show correlations of infection with ecological differences between plots. Owing to the present inaccessibility of the raw data, the recomputations of* χ^2 *must be postponed.—Author, Kew, March 1934.*

incipient lesions, and trees whose entire trunks are surfaced with infected bark from a continuous system of coalesced lesions studded with perithecia, and trees which have already died as a result of infection. In order to bring out differences between counties in the distribution of severity of infection, it was necessary to classify the *Nectria*-infected trees on the basis of severity of infection and to compare the distributions of percentages of infected trees in each class for the different counties. Such a comparison is presented in Table IV.

It will be seen from Table IV that the distributions of the percentages of beech with light, medium, and heavy infection are very similar for the three counties on the mainland of Nova Scotia; not only are the mean percentages themselves close in each class, but the odds expressing the probability of significance of differences in distribution, based on the actual tree counts, are small. The same situation holds for the two grouped counties in Cape Breton and New Brunswick. But the important fact emerges that the distribution for the Nova Scotia mainland differs from the distribution for Cape Breton and New Brunswick, and computation shows the probability of significance of difference to represent odds of more than 100 to 1. This is, of course, as was expected from accounts of the history of the disease in the Maritime Provinces and from preliminary observations. That is, in the examined areas on the Nova Scotia mainland infected for about 10 years, the mean percentage of the infected beech with light infection was found to be 7.4, with medium infection, 18.2, and with heavy infection, 74.4; whereas in the areas examined in Cape Breton and New Brunswick, infected for about four to six years, the mean percentage of the infected beech with light infection was 24.2, with medium infection, 31.4, and with heavy infection, 44.4. In other words, the percentage of infected beech with heavy infection was greater in the region attacked for approximately 10 years than in the region attacked for only four to six years, which means that this difference shows a satisfactory correlation with the period during which the disease is known to have been active in each of the two regions. These differences are shown graphically in Fig. 4.

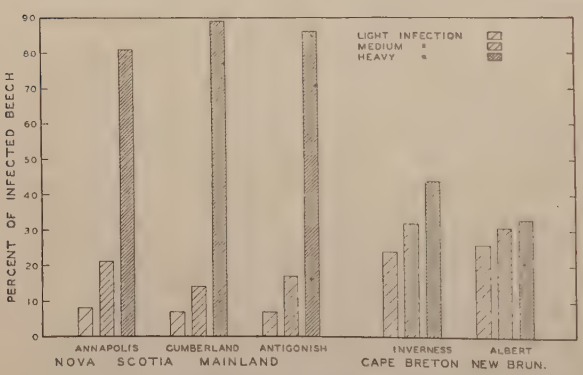

FIG. 4. *Percentages of Nectria-infected beech with light, medium, and heavy infection, in each county containing cruise areas.*

The most striking index to the effects of the disease, however, is actual mortality at time of observation. Mortality can be expressed in two ways, either as (1) the percentage of the total number of beech trees (stems) dead, or as (2) the percentage of the total volume of beech wood dead, indicated by the

TABLE IV

SEVERITY OF INFECTION OF *Nectria*-INFECTED BEECH, BY COUNTIES AND REGIONS

County or region	Mean per cent of total beech infected	Number of beech infected by *Nectria*	Per cent of infected beech			Probability of significance of difference in distribution of severity of infection*			Approximate duration of general infection in each region
			Lightly infected	Medium infected	Heavily infected	Between adjacently tabulated counties	Between Annapolis and Antigonish	Between regions	
Annapolis, N.S.	93.3	645	**8.1**	**21.1**	**70.8**	Between 49 and 99 to 1	Between 8 to 2 and 7 to 3	> 100 to 1	10 years
Cumberland, N.S.	88.0	411	**6.8**	**14.4**	**78.8**				
Antigonish, N.S.	89.7	304	**6.9**	**17.1**	**76.0**	Approximately 2 to 8			
Nova Scotia mainland, the three counties	90.8	1,360	7.4	18.2	74.4				
Inverness, (C.B.) N.S.	90.3	2,029	**23.7**	**31.6**	**44.7**	Between 1 to 1 and 7 to 3			4-6 years
Albert, N.B.	90.4	668	**25.7**	**30.6**	**43.7**				
Cape Breton and New Brunswick	90.3	2,697	24.2	31.4	44.4				

**These values are obtained by computing χ^2 according to a method in Fisher (1930 : p. 84-85, ex. 11) and converting into odds the values of P obtained by entering the χ^2 table.*

ratio which the basal area* of the dead beech bears to the basal area of all the beech. The first method gives a satisfactory index to the effect of the disease on the number of trees in a stand but, because size of tree is ignored, does not give an indication of the actual amount of damage in volume of timber. The mortality figures have been computed by both methods, taking the mean of the percentages for the individual plots, and are presented in Table V. The table shows that the data fall naturally into two groups which differ sufficiently from each other in the mean percentage of trees killed to justify their separation, but each of which is sufficiently homogeneous internally to warrant its handling as a group. Therefore, in subsequent analysis of mortality (Section VIII) the groups are treated separately. One group includes areas in Annapolis, Cumberland, and Antigonish Counties, Nova Scotia, with a mean percentage of beech dead of 48.0 by stems and 54.1 by basal area; the other, parts of Inverness County in Cape Breton Island, Nova Scotia, and Albert County, New Brunswick, with a mean percentage of beech dead of 19.2 by stems and 21.1 by basal area. The difference in percentage of mortality seems to be correlated with differences in the duration of the period in which the trees have been attacked by the pathogens, a situation reflected by the data on distribution of severity of infection (Table IV, Fig. 4).

It is further indicated by the table that for the regions examined the losses have been highest in Cumberland County, less in Antigonish County, and still less in Annapolis County. This suggests that the disease has been active longest in Cumberland County, for a shorter period in Antigonish County, and for a still shorter one in Annapolis County. This is in direct agreement with the data on distribution of severity of infection (Table IV, Fig. 4) and with the observations of foresters and others, and is in keeping with the fact that the disease has spread in all possible directions from the vicinity of Halifax. Similarly, the figures in the table are in agreement with the data on severity of infection and with observations in Cape Breton and New Brunswick, both indicating the presence of the disease for a somewhat longer period in parts of Cape Breton than in Albert County, New Brunswick.

Standard errors of the mean percentages of mortality for each county have been computed, and are low. The odds (see footnote 2 to Table V), contrary to those for percentage of beech infected, show the probability, that additional samplings would deviate more from the mean than those found, to be extremely slight, and thus indicate that the differences in percentage of beech killed from plot to plot are significant. This is expected from the fact that individual plot percentages range from 0 to 100, and suggests that the data for mortality should be analyzed further with a view to correlating the present percentage of beech killed with possible environmental or other factors. This subject is discussed in Section VIII.

**Basal area is total area at breast height (4.5 ft.) of the cross sections of all the stems. It is computed from the diameter by the usual formula:* $\Sigma A = \Sigma \left(\frac{\pi d^2}{2}\right)$, *where A is the area,* π *is 3.14, and d is diameter.*

TABLE V

PERCENTAGE OF BEECH DEAD, BY STEMS AND BY BASAL AREA (PLOT-PERCENTAGE MEANS), BY COUNTIES AND REGIONS

Regions		Nova Scotia mainland				Cape Breton and New Brunswick		
Counties		Annapolis	Cumberland	Antigonish	The three counties	Inverness	Albert	Both counties
Mean plot per cent beech dead by stems	Per cent beech dead	**44.2** ±3.7	**52.0** ±4.2	**48.6** ±3.9	**48.0** ±3.5	**19.9** ±2.0	**16.7** ±2.0	**19.2** ±1.7
	Probability odds*	<1 to 99	>1 to 99	>1 to 99	<1 to 10,000,000	<1 to 10,000,000	1 to 1	<1 to 10,000,000
Mean plot per cent beach dead by basal area	Per cent beech dead	**50.6**	**58.2**	**53.9**	**54.1**	**22.0**	**18.0**	**21.1**

**These values were obtained by computing χ^2 from the actual numbers of trees killed in each plot and the numbers expected, with a mean percentage of trees killed of 50 for the areas in mainland of Nova Scotia, and of 20 in Cape Breton and New Brunswick. The forumla is: $\chi^2 = \Sigma\left(\frac{x^2}{m}\right)$, where x is the difference between the actual and expected numbers of trees killed, and m is the expected number. Where n (the number of sample plots, minus 1) was 30 or less, the value of P was read from the χ^2 table in Fisher (1930) and these probabilities were then converted into odds. Where n was more than 30, the formula $\sqrt{2\chi^2} - \sqrt{2n-1}$ was used; and the value of P was read from Fisher's table of x.*

The values in this column measure the probability that additional samplings from the same population would show deviations as great as, or greater than, those in the present sampling.

The data on mortality are presented graphically by the diagonally ruled bars in Fig. 3, which shows additionally that although the time factor has little effect on the percentage of beech infected by *Nectria*, it bears a definite relation to mortality. It is evident that under conditions in the Maritime Provinces inoculation and infection take place rapidly but that mortality, although beginning promptly, extends over a period of years; it attained, in the areas examined, a magnitude of approximately 20% in four years and 50% in ten years. This is based on the reasonable assumption that climatic or other differences between the regions are not significant.

Table V shows further that mortality by basal area varies closely with mortality by stems, but is slightly greater (owing to omission of stems under four inches d.b.h.). If it could be shown that this correlation is constant and high for the data in the present survey, it would not be necessary to compute both figures in subsequent analyses of the data, since the values based on stems would be a sufficiently good measure of the damage expressed as basal area. Accordingly the values for each of the two regions were entered on a scatter diagram (Figs. 5, 6), on which the ideal perfect-correlation line is

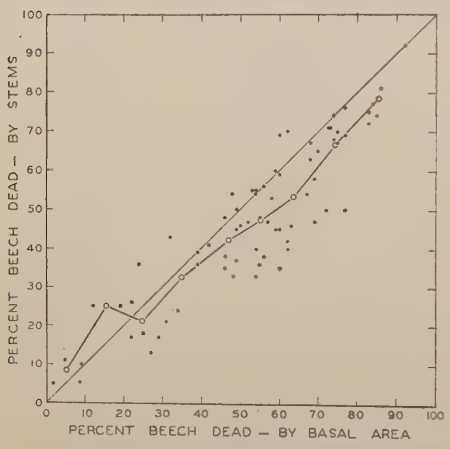

FIG. 5. *Comparison of percentage of beech dead according to number of stems, with percentage dead according to basal area; for plots in Nova Scotia mainland.*

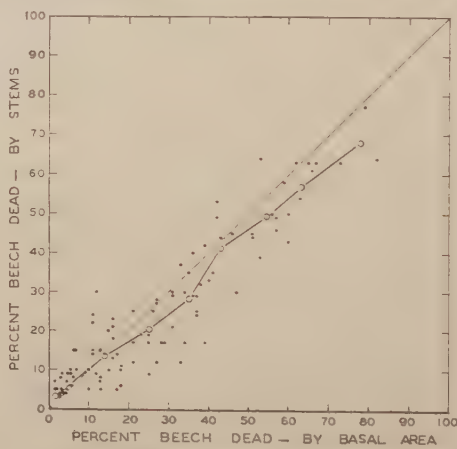

FIG. 6. *Comparison of percentage of beech dead according to number of stems, with percentage dead according to basal area; for plots in New Brunswick and Cape Breton.*

represented by the diagonal. The values according to basal area were arranged in 10% classes and class means obtained for basal area and for the stem values of the plots in each basal-area class. These mean points are plotted as circles on the diagram and show graphically the degree with which the mean of the actual plot points approximates to the ideal. The mean percentages of mortality by both methods, according to 10% basal area classes, are shown in Table VI.

It will be seen from Figs. 5 and 6, and Table VI that mortality (percentage of beech dead), expressed as stems, is closely correlated with mortality expressed as basal area. A statistical evaluation of this correlation is afforded by Pearson's coefficient of correlation r, which is computed from the data for

TABLE VI

PERCENTAGE BEECH DEAD BY STEMS: COMPARED WITH PERCENTAGE DEAD BY BASAL AREA, EXPRESSED AS CLASS MEANS ON THE BASIS OF PLOT PERCENTAGES

Region	Percentage beech dead by	Per cent classes of beech dead by basal area										Correlation coefficient r *	Probability of significance of r †
		0–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–100		
Nova Scotia mainland	Basal area	5.2	15.5	24.8	35.0	47.0	55.1	63.8	74.2	84.2 85.5	92.0	0.892 ±0.0025	Much > 100 to 1
	Stems	8.7	25.0	21.2	32.6	42.3	47.5	53.5	66.5	75.8 78.5	92.0		
Cape Breton and New Brunswick	Basal area	1.7	14.0	25.0	35.1	43.0	54.6	63.3	76.0 78.0	82.0	— —	0.922 ±0.0149	Much > 100 to 1
	Stems	3.1	13.5	20.3	28.1	41.3	49.4	56.9	70.0 68.0	64.0	— —		

*r is Pearson's coefficient of correlation and has been calculated by means of the correlation data sheet of Thurstone (1925: p. 202) according to the formula: $r = \dfrac{\frac{\Sigma xy}{N} - (dx \cdot dy)}{\sigma_x \cdot \sigma_y}$. The values of r range between -1.0 and $+1.0$, -1.0 indicating a perfect negative correlation, 1.0 a perfect positive correlation, and 0.0 no correlation whatever. The figure following $\pm$ is the standard error of r, calculated according to the formula in Fisher (1930: p. 158): $\sigma_r = \dfrac{(1-r^2)}{\sqrt{n-1}}$.

†These odds measure the probability that the computed value of r could not have arisen by chance, and thus are a measure of the degree of significance attaching to r. They are secured by computing t according to the formula in Fisher (1930: p. 159): $t = \dfrac{r}{\sqrt{1-r^2}} \cdot \sqrt{n'-2}$ and entering Fisher's table of t with n equal to two less than n', the number of the paired observations.

the individual plots; the values of r for each region are convincingly high and their standard errors assuringly minute. Another method of expressing the significance attaching to r is the odds that the computed value of r could not have arisen by chance; these odds are seen to be much greater than 100 to 1, and leave no doubt as to the degree of correlation.

In short, these data show that in the samples examined from widely separated regions the numbers of beech infected by the fungal pathogen were uniformly close to 90%, that the severity of infection was greater in regions attacked longer, and that mortality, although ranging for individual samples from 0 to 100%, attained a mean of approximately 20% in recently attacked areas and 50% in places exposed for a longer period. The data thus bear out the assertion that this disease has attained the proportions of a fatal epiphytotic which has already seriously depleted the beech stands of the Maritime Provinces, and represents an imminent danger of great importance to the beech stands of adjacent areas. When it is further realized (1) that mortality increases with size of tree (as discussed in Section VIII) and that, accordingly, the beech in the stand has been almost wholly destroyed so far as its merchantable value is concerned, (2) that loss of the older seed-bearing trees must lead to the curtailment of future reproduction, and (3) that the weakened, dead, and fallen trees provide ideal conditions for the building up of a dangerous host of insects and fungi capable of developing in the slash and weakened trees, it becomes evident that the disease is a serious matter.

VI. Symptomatology

A. GENERAL ACCOUNT

This disease begins with the infestation of the bark by the minute scale insect, *Cryptococcus fagi* (Baer.). The insect feeds by inserting its stylets (proboscis) into the bark, penetrating the corky layer, cork cambium, and phelloderm, and probing the underlying tissues of cortex and phloem, into which saliva is injected, and from which protoplasmic fluids are withdrawn. When populous colonies of the insect feed in localized areas on the bark surface, whole clusters of parenchyma cells are killed. These clusters dry and shrink, causing minute fissuring of the phellem and subjacent tissues. In regions where an abundance of inoculum of the *Nectria* has accumulated, these fissures quickly become inoculation courts and provide satisfactory substrata for incubation and initial infection of tissues normally resistant, by reason of phellar protection, to this fungus. Once established, the mycelium is able to spread beneath the phellem, invading phellogen, phelloderm, cortex, phloem, cambium, and the rays; growth is both inter- and intracellular in the susceptible tissues, but in the cork, in the nests of sclerenchyma of the older phloem, and in the non-living elements of the wood, mycelium is not found.

Light infestations of the insect and isolated fungal infections which do not enlarge rapidly frequently stimulate the suscept to the activation of a trau-

matic secondary meristem. This meristem leads to the formation of a hyperplastic tissue raised above the surface of the healthy bark. If this tissue is successful in cutting off the advance of necrosis with a resistant suberized callus layer, the infected area may be thrown off by the cracking of the margin of the lesion; if unsuccessful, the mycelium continues to radiate from the original infection court, killing all invaded cells and resulting in a disk-shaped circular lesion, somewhat sunken by the shrinkage of the dead tissues and frequently delimited at the margin by the cracking of the cork layer. When the lesion attains a periclinal diameter of one or two centimetres, the mycelium aggregates in the region of the phellogen and forms a band of pseudo-parenchymatous stroma which ruptures the phellem and results in the formation of pustules containing erumpent sporodochial proliferations of the stroma. On these sporodochia the hyaline elongate macroconidia (form genus *Cylindrocarpon* Wr.) are formed in dense clusters which appear to the unaided eye as loose white masses, resembling somewhat on superficial observation the woolly secretion of colonies of *Cryptococcus fagi*. Later, perithecia develop on the same stromata among the bases of the old conidiophores and, with the disappearance of the conidia, protrude from the pustules as globular red bodies.

Meanwhile, the continued advance of the mycelium leads to an extended zone of necrotic tissue which in time includes the cambium and inhibits further meristematic activity. The production of spores and consequent multiplication of the number of infections, combined with their periclinal enlargement, lead to the rapid coalescence of the individual necrotic lesions and the dying of large areas of bark, cambium, and young sapwood. These areas of bark become cracked with drying and shrinking, frequently loosen from the wood, and scale off in great sheets. On younger trees and in exposed locations where the fungus is able to develop less rapidly, where inoculations are less abundant, infections less successful, and fruiting less prolific, the general progress of infection is greatly retarded, individual lesions enlarge less rapidly and rarely coalesce, and a much smaller proportion of the vital tissues of the tree is killed. Under such conditions, continued meristematic activity of the cambium in the healthy areas results in the formation of depressions which are occupied by the lesions, and occasionally of cankers, some of which become eventually buried under callus rolls of new wood and bark.

The continued encroachment of the fungus on the tissues of the conducting and storage system of trunk and larger branches interferes increasingly with their functions and soon produces symptoms of moisture deficiency in the crown of the tree. As the growing season advances, foliage first curls, then dries, and becomes prematurely brown. Twigs and small branches become dry and many fail to produce buds. In the following spring, foliage is absent on many branches and the bark begins to crack. On other branches small chlorotic leaves develop, but they shrivel with the advent of hot dry weather. At this stage, large portions of the crown are already dead, the bark is loosening in patches on the trunk, and the end is near. The openings produced in

the crown canopy now retard the activities of the fungus by reducing the moisture both in the lower atmosphere and in the bark; but they also remove moisture more rapidly from the soil and leave less available to the tree. A few of the heavily infected individuals are able to survive this drought and profit by its inhibitory effect on the fungus. Most trees soon die.

B. SIGNS

The Insect

In an infested area, countless numbers of minute yellow larvae of *Cryptococcus fagi* can be detected by scrutiny of the bark during the months of August and September. By late autumn many of these larvae settle in sheltered positions on the bark, insert their slender and powerful stylets, and secrete from numerous glands a wax which is exuded in long curly threads and soon envelops them in a fluffy white down. The numbers of insects increase year by year and individual insects are replaced by colonies; the colonies grow numerous and populous, and the secretions of white wax form a continuous mass of "wool," interspersed with the shrivelled bodies of annual generations of exhausted females. Eventually under favorable conditions the trunk and branches appear at a distance as though coated with driven snow. Although in sheltered stands the insect can feed on any portion of the trunk and on the undersides of the larger branches, the densest masses of "wool" occur in lenticular crevices, in cracks and wounds, under mosses and foliose lichens, and in the abaxillary angles of the lower branches. A light young infestation in lenticular crevices and old superficial wounds on the trunk of an ornamental specimen of *Fagus sylvatica* is shown in Plate II, Fig. A; an older and heavier infestation on a forest beech *(F. grandifolia)*, still following in general the lenticular crevices, but covering almost all except heavily corked areas, appears in Plate II, Fig. B; somewhat enlarged views showing the depths which the woolly mass attains with increasing infestation may be seen in Figs. C and D. Still greater enlargements show how on exposed bark the colonies begin in lenticular crevices (Plate II, Fig. E), and how the individual threads curl and interlock to form a deep but light and resilient canopy over the insects nestling beneath (Plate II, Fig. F). With advent of the fungus, the tissues on which the insect depends for nourishment are killed, the current generation of insects dies, and in time most signs of the infestation disappear.

The Fungus

Following infection of the bark in a minute fissure developing after feeding by the insect, the mycelium radiates periclinally under the phellem. After a time pseudoparenchymatous aggregations of hyphae are formed in the region of the phellogen and can be seen as orange-colored masses by shaving the corky layer. Later, they become erumpent in a ring, from one to two centimetres in diameter, of white sporiferous pustules (Plate III, Fig. A), this ring being situated centrad of the periphery of the mycelium. The corky layer of the bark is broken usually without the loss of the upturned edges,

which remain surrounding the sporodochium (Plate III, Fig. B). The maturing macroconidia are released from the conidiophores and borne away by wind and rain; meanwhile, perithecial initials have been forming at the surface of the stroma and with the passing of the conidia are elevated among the remnants of conidiophores, and stand in clusters that obscure the stromata from which they spring (Plate III, Figs. C, D). With heavy inoculation and conditions propitious to uniformly rapid inoculation, incubation, infection, and fruiting, the numbers of perithecia developed are so enormous that the trunk of a severely attacked beech, especially when wet, sometimes appears red with perithecia. This is particularly striking when fresh perithecia form promptly on the areas between the original circular lesions, newly infected by the advancing mycelia, so that square metres of bark surface are uniformly studded with close packed clusters of these small, bright red fruiting bodies.

As asci and ascospores mature, the perithecia swell, rising above the bark and crowding one another, so that many central ones either remain lower than the majority or else become laterally compressed, and many marginal ones are forced beyond the original limits of the pustule (Plate III, Figs. D, E). The apex of the perithecium becomes slightly drawn out into a papilla which contains a structurally organized ostiole through which the ascospores are discharged. When the perithecium first becomes wet, discharge is violent, but with the passing of time and the thorough wetting of the bark and perithecium the spores are forced by swelling of the ascus into the ostiolar canal in such numbers that they jam and ooze out, first in a spore plug (Plate IV) which becomes a delicate curling tendril, later as a formless mass which covers the apex of the perithecium and frequently remains with drying *in situ* until the next rain. When most of the ascospores have been discharged the upper half of the perithecium collapses and sinks into the lower half, much like a deflated rubber ball, so that the empty perithecium sometimes resembles superficially the fructification of a discomycetous fungus (Plate III, Fig. F). The color of the first emergent perithecium is a bright red, of the old discharged one, a dark fuscous red. Within a year after discharge, weathering usually reduces the cluster of perithecia to a few drab, dark colored, formless remnants.

Trees weakened by prolonged insect infestation and by *Nectria* infection are frequently attacked by weak parasites and saprophytes which may increase the pathological effects and produce disintegration of the infected tissues. The most common of such organisms in the Maritime outbreaks are *Scolytid* bark beetles, and fungi. A beetle is occasionally seen crawling on the surface of the bark and boring into the centre of a young circular lesion; more often only the entrance to its tunnel is visible, usually plugged with a core of frass which may protrude for a distance of almost a centimetre from the surface of the bark. The commonest of the fungi are species of *Hypoxylon* which are occasionally able to grow in living bark and produce broad shallow cankers; their brick red to brown or black superficial stromata are conspicuous over large surfaces on dead areas of bark. Other fungi whose fruiting

bodies are encountered commonly on dying or dead bark are members of the Thelephoraceae (especially species of *Stereum*), Dacryomycetales, Agaricaceae, and Polyporaceae (especially *Fomes fomentarius* L. ex. Gill., *F. igniarius* L. ex. Gill., and *F. applanatus* Pers. ex Wallr.).

C. MACROSCOPIC SYMPTOMS

On Infected Bark

Dying of lichens and mosses. Discoloration and death of the mosses and foliose lichens which abound on the trunks of beech in the Maritime forests are among the first symptoms of infection visible to the unaided eye. The first colonies of the insect and the first fungal lesions develop on the bark beneath moss and lichen thalli. The epiphytic habit of these plants precludes the possibility that mere death of their substrata exerts a lethal influence; a more likely, but as yet unsubstantiated, explanation is that the fungus itself produces diffusible substances toxic to the epiphytes; the production of such toxins is suggested also by the death of bark cells adjacent to fungal hyphae but which the hyphae do not penetrate, and by the death of cells some distance in advance of the mycelium. When infection takes place under conditions not highly favorable to the fungus, a lesion frequently remains restricted to the area covered by the lichen thallus, becoming and remaining depressed with the continued growth of the surrounding healthy tissues (Plate V, Fig. D).

Bark lesions. Death of the infected bark is followed by desiccation and shrinkage, so that when seasonal changes cause a temporary cessation of mycelial advance the circular zone of necrotic tissue becomes slightly depressed and sometimes cracked both internally and about its margin; simultaneously, the pressure of stromatic aggregations produces pustules whose edges are formed by upturned phellem, first in a ring some few millimetres within the margin of necrosis, and later throughout the central zone (Plate V, Fig. B). When the mycelium resumes growth the lesion enlarges periclinally and coalesces with adjacent infections, resulting in large, irregularly shaped, necrotic areas which become covered indiscriminately with pustules and develop larger and deeper cracks, penetrating ultimately to the cambium; on such areas the limits of the original circular lesions are sometimes still discernible (Plate V, Fig. A). Finally, the drying and shrinking of extensive areas of bark produces long vertical cracks connected here and there by horizontal ones; loosening of the bark from the wood by death of the cambium leads to the scaling off of roughly rectangular sheets which fall away, exposing the drying and splitting wood of the trunk (Plate VI, Fig. E).

The local necrosis and fissuring produced by the insect expose the susceptible inner tissues to infection not only by the pathogenic *Nectria* responsible for most of the injury but to a host of other organisms. Certain of these are purely saprophytic and grow only in the dead tissues, disintegrating, digesting, and fermenting them to a watery or slimy mass which oozes from the surface of the bark and seeps down as a discoloring liquid. Such a lesion

(slime flux) has a characteristic odor reminiscent of certain organic acids. The decomposition products of these activities evidently contain substances toxic to the living tissues of the bark, because discoloration and death of the cells extend for a considerable distance beyond the area occupied by the micro-organisms and may ultimately involve several square centimetres of bark surface. A cavity penetrating to the wood is common at the centre of the slime flux and is a favorite point of entry for *Scolytid* beetles and rendezvous for sow bugs (Oniscoida).

Cankers. On younger trees and on bark in open stands the number of infections is much smaller than in the dense forest. The same factors that determine this situation apparently also weight the odds in the combat between pathogen and suscept in favor of the latter. Individual lesions remain more nearly circular, enlarge slowly or not at all. Occasionally they are thrown off by formation of a corky layer which circumscribes and isolates the infected tissues, raising them as a disk which may rupture (Plate V, Fig. C), and eventually causing them to slough off. More often the continued growth of surrounding healthy meristems encircles the infected zone with a callus of new bark and wood. In the early stages of the process, pustules and fructifications of the *Nectria* can still be seen on the infected bark. Later, these signs and symptoms disappear and the lesion becomes a deeply depressed cavity surrounded and partially or completely healed over with callus. Stems supporting many such lesions become pitted and gnarled (Plate V, Figs. E, F). This process does not usually result in a typical scalariform canker, probably because the fungus is unable under such conditions to keep pace with the active meristems of the suscept.

Internal necrosis. The infected tissues of the bark beneath the phellem change in color from their normal pale yellow to a pale orange red and later to a dark red which becomes tinged with brown on drying. The first infections are usually superficial so that shaving the bark to a depth of three or four millimetres removes all necrotic tissue. In time, with the spread and penetration of the mycelium, the necrotic areas coalesce and penetrate in the old centres into phloem, cambium, and sapwood. Removing all tissues above the cambium in such an area exposes the surface of the sapwood (Plate VI, Fig. D) which has been reached in a number of points by the advancing mycelium, but in only one of which a sufficiently large area of cambium has been destroyed to leave a disk of red necrotic tissue surrounded by newly formed sapwood. With active infections, areas such as this one enlarge and coalesce with others until the conducting tissues are effectively interrupted by a series of vertically overlapping cambial lesions. This condition interferes with conduction of water and inorganic salts, of elaborated organic foods, and with storage of the latter in both phloem and xylem, all exerting a critical inhibitory influence on the normal metabolic and meristematic activities of the entire tree.

On young or isolated trees the individual circular lesions enlarge but little and are frequently walled off by callus and then either sloughed off by being

raised, or else buried. A series of views of two small sunken lesions on a young stem is shown in Plate VI, Figs. A, B, C. Fig. A shows the surface aspect with the bark cracked across the face and with the borders raised in rolls of newly formed bark and wood. Shaving to the depth of the bark in the depressed necrotic areas (Fig. B) exposes the new wood; the necrotic areas are dry and brown-black; the borders which still support active infection are light red; and the surrounding healthy wood is a pale yellow. At a depth of three eighths of an inch (Fig. C) the lesions are still visible in the wood and show by their dark color and by the curving contour of the healthy wood outside that they have been present but relatively inactive for a number of years. A similar condition exists in lesions on older trees which have become exposed subsequent to infection by the opening of the crown canopy.

On the Crown

The destruction of protective, vascular, and storage tissue-systems of the trunk leads to a progressive killing of the tree, accompanied by striking symptoms in its crown. When they first appear late in the growing season, these symptoms are usually diagnostic of water deficiency. Leaves, which could be kept turgid earlier in the season, curl and become prematurely brown. The twigs dry; no buds are formed; the dead leaves adhere and weather through the winter. In the following spring, these and other branches remain bare and twigs begin to break off. Other branches, undersupplied with stored food, put out chlorotic undersized leaves which may or may not survive the summer. The large crown openings which result expose the remaining foliage to sun and wind to a greater extent than normally; this increases even more the demands on a rapidly disintegrating vascular system. The partial girdling of beech by porcupines, common in parts of the Maritime Provinces, serves to intensify the crisis. With the loss of foliage and stored organic food materials, the roots dry and decay, conduction comes to an end, the remaining uninfected living tissues die of water deficiency, and the progressive killing of the tree is complete. A *Cryptococcus*-infested beech ridge in Inverness County, Cape Breton Island, which was infected heavily by the *Nectria* but a year or two before being photographed, is shown in Plate I. Certain of the trees died during the previous year and are leafless. Others were able to leaf-out, but renewed activity of the fungus completely disrupted vascular activity and the foliage dried and became brown. Others still support a chlorotic verdure, and only a few show vigorous healthy crowns. Other views in attacked stands appear in Plate VI, Figs. F, G. Fig. G, taken along a newly cut highway in Cumberland County, Nova Scotia, shows young and old beech plucked by the disease, with nothing but maples remaining. Fig. F is from Annapolis County, Nova Scotia, and shows a similar condition.

D. MICROSCOPIC SYMPTOMS

Feeding by Cryptococcus fagi

Although there has been considerable study of the histological aspects of the effects of sucking insects on leaves and stems, only Hartig (1880) and Boodle

and Dallimore (1911) have reported observations on *Cryptococcus fagi*. Hartig apparently made no study of the relation of the suctorial apparatus of the insect to the plant cells, but noted that the stylets are able to penetrate to the green bark parenchyma and stimulate the production of a radially arranged, thin-walled gall parenchyma by meristematic activity of the parenchymatous elements of bark and phloem. In young trees this leads to a tearing of sclerenchyma nests and the formation of superficial galls. Small galls remain closed; larger ones burst and expose the wood, which dies and, by the accumulation of decomposition products, develops longitudinal brown streaks. In older trees the greater sclerenchymatization prevents gall formation, but the killing of parenchyma cells produces browning and drying, which lead to tearing of the bark. Boodle and Dallimore (1911) observed the sucking tubes of the insect in the outer tissues of the bark, sometimes reaching to a depth of one millimetre. They noted differences in the amount of sclerotic tissue and of cell contents in the phloem, but failed to correlate the presence or abundance of *Cryptococcus* with these conditions.

Although the writer encountered technical difficulties in preserving the insects *in situ* during washing and embedding, in softening the sclerenchymatous tissues without injury to the delicate parenchyma, and in sectioning, a satisfactory technique was ultimately devised which yielded thin sections of well preserved material. Blocks of infested bark were cut from the tree and either the top surface dipped into hot wax or celloidin or the entire block wrapped in perforated waxed paper. Fixation was best in weak chromo-acetic solution and in Carnoy's fluid. After removal of the reagent the siliceous materials were partly dissolved in hydrofluoric acid diluted with 30 or 50% ethyl alcohol. After washing, and dehydration by the butyl alcohol series, the blocks were embedded in nitrocellulose (preferably Mallinckrodt's Pyroxylin) and sectioned with a sliding microtome. The most useful stains were safranin and light green followed by mounting in balsam, and acid fuchsin in lactophenol.

The stylets, or portions of the suctorial apparatus which are inserted into the plant, consist, as with other Homoptera, of the maxillae and mandibles modified into four slender and flexible grooved filaments which are held appressed to form a double-tubed pump. One channel pumps saliva from the salivary glands; the other sucks up fluid materials from the punctured plant cells, mixed with saliva. The stylets attain a length in adults of almost 1500μ. They can reach into the outer phloem in young bark, but extend most commonly into phelloderm, adjacent cortex, and pericycle. The phellar layer is usually penetrated perpendicularly without visible tearing and apparently without being dissolved (Fig. 7). In the phelloderm and within, the course is not fixed, being sometimes parallel to the axis of the stem, and sometimes tortuous. An adult rarely penetrates the corky layer more than once, but probes internally in all directions by branching from the original path and from laterals. The walls of living cells, unless sclerotic, do not obstruct the stylets; penetration is intra- as frequently as intercellular

(Figs. 7, 8; Plate VII, Figs. D, F, G). Only when a nest of stone cells is encountered do the stylets either stop or attempt to circumvent the obstruction (Plate VII, Fig. C); occasionally progress is made between the cells of such a nest (Plate VII, Figs. A, E).

The course of an insect's probing is fortunately marked by the formation of a permanent structure, the stylet track. This consists of the hollow or precipitate-filled stylet-sheath, which remains after the stylets are withdrawn, as a permanent record of their course. The composition of this material is not known; it stains strongly with both safranin and acid fuchsin. The sheath appears to be two-layered, consisting of a narrow, uniform inner lining which is in contact with the stylets while they remain, and a thick irregular outer material, deeper over the portions of the sheath within the plant cells than in the intercellular portions, and deeper in living parenchyma cells than in dying cork cells (Figs. 7, 8). The inner lining sometimes protrudes somewhat above the surface of the bark (Fig. 7). These characteristics suggest that a component of the lining is secreted by the insect and covers the surface of the stylets, while the outer material is precipitated by the reaction of the contents of the punctured cells with this material or with a constituent of the saliva.

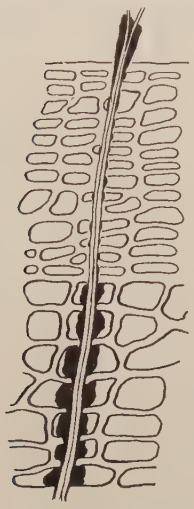

FIG. 7. *Stylets and stylet track of Cryptococcus fagi in periderm of Fagus grandifolia.*

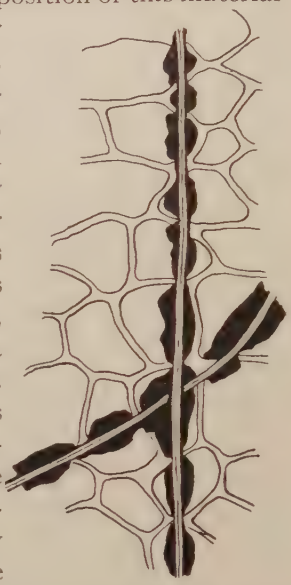

FIG. 8. *Stylets and stylet tracks in bark parenchyma.*

The contents of punctured cells are shrunken and killed, but no pathological effects seem to extend at first beyond the injured cells, suggesting that the saliva contains no violently toxic constituents capable of diffusing from the immediately probed point into neighboring cells. With continued feeding of large numbers of individuals at a localized point, the entire area dies and shrinks and cracks. The area becomes brown and the browning extends to surrounding unpunctured cells. The whole is frequently surrounded by a meristem which builds a wall of radially arranged parenchyma cells; these sometimes become suberized, isolate the area, and cause the ultimate death by starvation of the feeding insects. In spite of the protection afforded the insects by lenticular shelves of cork (Plate VII, Fig. B), the lenticels on sheltered bark are not probed as abundantly as the interlenticular surfaces, probably because the greater depth of loose phellar sheets in the lenticels increases the difficulty of reaching succulent tissues.

Infection by Nectria

When ascospores or conidia of the *Nectria* are deposited in the cracks which form in the bark subsequent to feeding by *Cryptococcus fagi*, their germ hyphae are able to enter the exposed parenchyma tissues of phelloderm and cortex and grow both inter- and intracellularly, occupying the fissures which have resulted, and sending hyphae into the living tissues. The nests of stone cells are occupied only intercellularly but other cells are entered and killed (Fig. 9). The walls of the dead cells collapse and form a moist red-brown mass, the interstices of which become filled with broad, irregularly swollen, short celled hyphae of a pale yellow color. Tissues some distance beyond the visible limits of the mycelium die and become brown, suggesting toxic substances, produced by the action of the fungus on the bark cells. Meanwhile, mycelial aggregations form dense pseudoparenchymatous stromata in the phellogen and press outwards against the phellem which eventually ruptures (Plate VIII, Figs. A, B, D). As the stroma rises to form a sporodochium, indications of its hyphal nature are obliterated and the cells become rhomboidal in longitudinal outline and form a pseudoparenchyma. The topmost cells elongate and become conidiophores on which the long, slightly curved, four–seven-septate, hyaline macroconidia are borne (Plate VIII, Figs. C, E). As the conidia are released, perithecial initials take form in the upper portion of the stroma and become elevated by an elongation of their basal cells (Plate VIII, Fig. F).

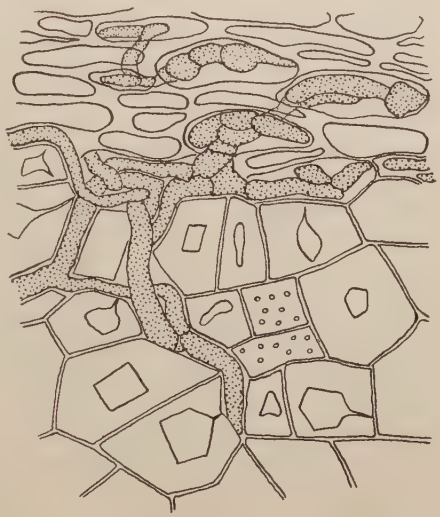

Fig. 9. *Nectria mycelium penetrating bark-parenchyma cells, but intercellular among stone cells.*

VII. Etiology

A. THE INSECT

Nomenclature

Common Names

By far the greatest number of references to *Cryptococcus fagi* have been made in Germany and Great Britain. In Germany, probably the earliest common name known to be applied to the insect is in the reference which Ratzeburg (1869) made to a species of "Schildlaus" (genus *Coccus*) on beech, discovered by R. Hartig. Hartig himself referred to it as the "Buchenwolllaus" (1878) and the "Buchen-wollaus" (1880); the latter name was used by Altum (1881); similar designations were "Buchen-Woll-Laus" (Schröder 1897), "Buchen-Wollaus" (Bertelsmann 1913 a), and "Buchenwollaus" (Bertelsmann

1913 b). Sinz (1913, 1914) used the latter two names erroneously for the aphid, *Lachnus exsiccator* Alt. *(L. fagi* L.), and drew attention to the confusion which can arise in common German names of the bark infesting coccid *Cryptococcus* with the leaf sucking aphid, *Lachnus*. The name "Buchen-Wollschildlaus" was first used by Judeich and Nitsche (1895) and later by Nüsslin (1905, 1913) and by Eckstein (1920); Rhumbler's (1914 a, 1914 b, 1915, 1922, 1931) "Buchenrinden-Wollaus" is perhaps the most descriptive and least confusing of the German names.

In Holland the insect has been called "Beukenwolluis" (Anon. 1921), and in Sweden, "Boksköldlusen" (Trägårdh 1921).

In Great Britain the insect has been known longer than in Germany, although the first published reference at hand, by M'Intosh (1849), spoke of it as a white, rapid-spreading fungus. As late as 1860 Berkeley still mistook it for a fungus, although he later corrected this impression (Berkeley 1865) and two years later referred to the insect as the "coccus" (Berkeley 1867). It had been recognized as an insect as early as 1850 by some (C.C., M'Intosh, Hardy) and was rather well described by Hardy (1850). Nevertheless, it was not until 1898 that Miss Ormerod pointed out that no common English name was yet in general use, and suggested "beech-bark 'felt-scale'," a name subsequently used, to the present writer's knowledge, only by Gillanders (1908). This name apparently met with little approval, for two years later Newstead (1900) called it the "felted beech coccus"; and this name has since been in common use (Boulger 1907, Webster 1908, Munro 1925, Forestry Commission 1926). Other British names are "woolly scale of the beech" (Carpenter 1903), "beech-felted scale" (MacDougall 1908), and "beech coccus" (Boodle and Dallimore 1911).

In Canada the first reference is by Braucher (1914), who quoted from a letter in which Dr. L. O. Howard stated that a Mr. Sanford had identified the specimen in question as the "European felt scale." The Dominion Entomologist used Newstead's name "felted beech coccus" (Hewitt 1914), as did Gorham (1929) and Gorham, Walker, and Simpson (1929). Subsequent designations were "the imported beech bark-louse of Europe" (Motherwell 1926), "beech bark louse" (Graham 1927), "European beech coccus" (Swaine 1930), "beech coccus" (Balch 1932, Ehrlich 1932 b).

In the United States the common name approved by the American Association of Economic Entomologists (1930) is "beech scale." This name has accordingly been used by Schaffner (1931), Collins (1931, 1932), Peirson (1932 a, b), and Ehrlich (1932 a, 1933), although the woolly character of the waxy secretion, which is not very common in scale insects, seems, in the opinion of the present writer, to justify and call for the name "woolly beech scale."

Latin names

It has been generally conceded by entomologists that Baerensprung (1849) was the first to recognize the woolly beech scale as an insect and named it

Coccus fagi. But entomologists seem to have overlooked the fact that the mycologist Fries (1832) had observed the woolly secretion of this insect some 20 years previously, had assumed that it was fungal in nature, and had published a name and description. He placed it in his genus *Psilonia*, Fungi Imperfecti, class Hyphomycetes, order Sepedoniei, and named it *Psilonia nivea*. This regrettable error was recognized early by some mycologists, but was propagated unknowingly by others through the remainder of the nineteenth century. Although the writer has not personally examined type material and although Fries mentioned spores, the writer is convinced that Fries actually had before him none other than the "wool" of *Cryptococcus fagi*, occupying crevices in the bark of *Fagus sylvatica*.

In 1838 Libert distributed, in her "Plantae cryptogamicae quas in Arduenna collegit," specimens marked *Psilonia nivea* Fries; the writer has been privileged to examine these in the Farlow Herbarium, and found no fungus but the "wool" and shrivelled bodies of the beech scale. A second notice of *Psilonia nivea* appeared in Fries (1849). Berkeley and Broome include *Psilonia nivea* Fries among British fungi and note that it is "remarkable for its curled flocci, which sometimes resemble unrolled spiral vessels" (1859 : p. 361). It is mentioned again the following year (Berkeley 1860). Following this, Berkeley evidently became aware of the entomological nature of his material: in 1865 we find him writing to a correspondent of the Gardeners' Chronicle: "The white substance on your Beech bark has been included amongst Fungi under the same of Psilonia nivea, but it is an insect production . . . . " (Berkeley 1865 : p. 776). Two years later he quoted a letter from Professor C. C. Babington in which it is stated that he found the bark of his beeches covered with the "coccus," "which produces a quantity of white smooth hyaline threads which are often mistaken for a Fungus, and were described as such under the name of Psilonia nivea by Professor Fries. . . . . " (Berkeley 1867 : p. 235-6). In the same year Kickx published a description, under his family Byssoïdées, of the "fungus" *Psilonia nivea* Fries, obviously based on the original description and the Libert exsiccatus, and appended the following remark: "On trouve souvent entremêlées aux acrospores . . . . des globules microscopiques, qui paraissent être des conidies" (Kickx 1867 : p. 285). In 1871 Cooke stated: "*Psilonia nivea* Fr. is clearly an insect production" (p. 624). In 1880 Lambotte admitted: "Quelques auteurs croient que cette espèce (*Psilonia nivea* Fries) est une production des insectes" (p. 256).

When Saccardo placed certain of Fries' species of *Psilonia* in the genus *Volutella*, he included *V. nivea* (Fries) Sacc., with *Psilonia nivea* Fries as a synonym, edited Fries' description, and—evidently overlooking Berkeley's earlier correction (1865, 1867)—concluded with the opinion: "Sec. Cooke est opus insectorum, quod vero descriptio auctorum non confirmat" (Saccardo 1886 : p. 685). It seems evident that he referred to Fries' original description, and that he accepted it as referring to a fungus. Two years later, Cooke stated that *Volutella nivea* "is *Adelges Fagi*, according to authentic specimens"

(1888 : p. 13). Thus it can be asserted reasonably that the name *Psilonia nivea* applies, if not to the woolly beech scale itself, to an integral part of it. Cooke's statement was compiled without comment by Saccardo (1892), and was accepted by Massee (1893). *Volutella nivea* (Fries) Sacc. was included in the fungal flora of Belgium by De Wildeman and Durand (1898). As late as 1909, Lindau listed *V. nivea* as a fungus on the bark of *Fagus*. He also made two erroneous assumptions: first, in quoting Cooke's statement, he assumed that *Psilonia nivea* Fries is the product of a leaf-sucking aphid, apparently because the aphid *Phyllaphis fagi (=Adelges fagi, pro parte)* actually occurs on beech foliage, although Fries stated: "E rimis corticis Fagi" (1832 : p. 450), and Cooke likewise stated: "On bark of *Fagus*" (1888 : p. 13); second, he believed that Saccardo had actually examined and described other material of true fungal nature—a conclusion which does not follow from Saccardo's (1886) own statement. Finally, Weese (1931) evidently also accepted Cooke's claim.

In short, it is held by the present writer that the "fungus" described by Fries under the name *Psilonia nivea* is the wool-like waxy secretion of the beech scale and as such deserves discussion in a historical résumé of the nomenclature of this insect; this decision is based on (1) Cooke's statement that he examined an authentic specimen from Fries, and (2) the fact that the Libert exsiccatus specimen (1838, No. 387) examined by the present writer consists solely of the "wool" and shrivelled bodies of the woolly beech scale on *Fagus* bark. Although the fungal nature of *Psilonia nivea* was attested to—without careful examination—by Berkeley and Broome (1859), Berkeley (1860), Kickx (1867), Lambotte (1880), Saccardo (1886), De Wildeman and Durand (1898), and Lindau (1909), its insect origin was recognized by Berkeley (1865, 1867), Cooke (1871, 1888), Massee (1893), and Weese (1931).*

The first generally recognized reference to the woolly beech scale as an insect is by Baerensprung (1849), whose description is perhaps inadequate according to present standards but leaves no doubt as to the identity of the insect which he recognized as an undescribed species of the genus *Coccus* and named *C. fagi*. This was in Germany. Late the same year in Scotland M'Intosh (1849) mentioned a white, rapidly spreading fungus, giving the bark of trunk and branches the appearance of being covered with snow; his own subsequent statement leaves no doubt that this "fungus" is no other than the woolly beech scale. A few weeks later C.C. (1850 : p. 11) stated that the disease referred to in 1849 " . . . . is caused by one of the Aphides *(Aphis Fagi)*, which attacks the bark of the Beech . . . . "; he neglected to mention whether this name is his own or an old one. In an editorial comment appended to C. C.'s communication, M'Intosh observed that Balfour also considered the disease to be of animal origin, "probably a species of *Coccus*" (C.C. 1850 : p. 11). A few weeks later in the same journal M'Intosh (1850 : p. 45) pointed out that "The Aphis Fagi is, we believe, always found on the

**It is hoped that this unfortunate error—whereby a secretion of an insect, being mistaken for a fungus, was given mycological status and a technical name—will not be seized upon in future by some ardent taxonomist of insects, and the name Psilonia nivea Fries held up as the one and true name for the woolly beech scale.*

foliage of the Beech, not the bark." Later the same year Hardy (1850) published a detailed and rather good description of the insect. He pointed out that it was obviously not a member of the "Aphidae," but probably one of the Coccidae, and that his description of the egg and larva corresponds with that of "certain young *Cocci*" and also with that of the related "*Lecanium* or *Chermes*." He quoted from a letter written near London by Walker: "1847 was I think the first year in which a cottony substance appeared on the trunks of Beech trees . . . . It is a *Coccus* much resembling the white bug *(C. Adonidum)* in houses, and as nearly allied to *C. Quercus* . . . . " (Hardy 1850 : p. 170). Walker wrote further that as this insect appeared to be unnoticed by authors he suggested calling it *Coccus fagi*—the very name which Baerensprung (unknown to Walker) had already employed. Two years later—apparently still unaware of Baerensprung's account—Walker (1852) published a brief description of the insect from specimens in the British Museum, under the name *Coccus fagi;* this name was accepted by Balfour and by Hardy, who wrote to Balfour: "The cottony substance sent is produced by Coccus fagi Walker . . . . " (Balfour 1863 : p. 267-8). An unsigned editorial reply to R. T. P. (1858) in the Gardeners' Chronicle stated that the insect in question—which was undoubtedly the woolly beech scale—is "the *Psylla Fagi*," without including either the origin of the name or a description of the insect. In 1870 A. M. noted that "the piece of beech bark sent is completely covered with the white excrescence of a Coccus, Adelges fagi . . . . " (p. 389). As with other such notes, neither the origin of the name nor a description of the insect was included.

Meanwhile in Germany, Ratzeburg, in the sixth edition of his "Waldverderber" (1869), had mentioned a species of Schildlaus in the genus *Coccus* discovered by R. Hartig on beech. In 1872 Kaltenbach, under the designation "? Chermes fagi n. sp.," gave notes on description and life history of an insect on beech which formed a woolly weft much like that of *Chermes corticalis* Kalt. on Weymouth pine *(Pinus strobus* L.); although Kaltenbach thus evidently assumed this insect to be an aphid, there is little doubt that he dealt with the woolly beech scale. This is indicated by the fact that his countryman Hartig (1880) discussed and figured what is unquestionably *Cryptococcus fagi* under the name "*Chermes fagi* Kltb." In previous accounts, however, Hartig referred to this insect as *Chermes fagi* Ratzeburg (Hartig 1876) and merely as *Chermes fagi* (Hartig 1878). In 1881 Altum—unaware of any previous descriptions—gave notes and sketches of the same insect and, apparently because of its superficial resemblance to species in Kaltenbach's genus Chermes (in respect to the woolly secretion), called it by the very name which Kaltenbach—unknown to Altum—had used, namely *Chermes fagi.*

Meanwhile Signoret (1873), chancing on a short description of "*Coccus fagi*" published by Hardy in 1864, for which a cottony down is mentioned, wondered if Hardy meant the "aphis du hêtre" and tentatively renamed it "*Pulvinaria ? fagi* Hardy." Having meanwhile discovered Baerensprung's (1849) and Walker's (1852) reports, but having apparently never seen a specimen of the insect, Signoret (1876) presumably reconsidered his guess of three

years previous and now guessed that this species should be placed in his genus *Pseudococcus*. A decade later Douglas (1886) reviewed the accounts of Signoret (1873, 1876), Hardy (1885 a, b), Baerensprung (1849), and Walker (1852), and concluded his remarks with the following temporary acceptance of Signoret's *Pseudococcus fagi*.

"The genus *Pseudococcus* Sign., is not exactly the same as the original *Pseudococcus*, Westwood, ... but not to argue nor to put too fine a point on the matter, the genus, in either case, may be regarded as, like Mercutio's wound, not of strictly definite dimensions, and like it also—''tis enough, 'twill serve'—for this occasion" (Douglas 1886 : p. 154). But by 1890 Douglas had reconsidered the matter, and published the following curt and incisive statement, which was destined to launch the now generally accepted new genus *Cryptococcus:* "the species *Coccus fagi*, Baerensp., hypothetically referred by Signoret to *Pseudococcus* (cf., Ent. Mo. Mag., xxiii, p. 153), has nothing to do with that genus, and as it does not accord with any other, I suggest for it a new genus, CRYPTOCOCCUS; the characters are included in those of the species, *l.c.* It may have some, but not close, affinity with *Xylococcus*, F. Löw (Verh. k. k. zool.-bot. Gesells. Wien, 1882, p. 274); at present the position of both is doubtful." (Douglas 1890 : p. 155.)

With the exception of the careless confusion by Schröder (1897) of the apple aphid *(Schizoneura lanigera* Housm.) with the woolly beech scale, and of Nüsslin's conservative use of *Coccus fagi* Baerensprung in 1905 and Barbey's in 1913, all subsequent authors, including monographers of the Coccidae, have accepted Douglas' genus and refer to the woolly beech scale as *Cryptococcus fagi* (Baerensprung).*

The foregoing annotations to the nomenclature of *Cryptococcus fagi* are summarized in the list which follows. Here names proposed by their authors as new are in bold face type; names questioned by their authors are preceded by the question mark (?). Names in brackets ([ ]) were thought by their authors to refer to a fungus. The dates in parentheses (()) refer to the year of publication (the references being cited at the end of the paper). When the authority following the colon (:) is in parentheses, he accepts the generic name given; when either authority is without parentheses, he is responsible for the generic name.

Chronological Summary of Latin Names

[**Psilonia nivea** Fries (1832)]
[*Psilonia nivea* Fries : (Libert 1838)]
[*Psilonia nivea* Fries (1849)]
Coccus fagi Baerensprung (1849)
[fungus (not named) M'Intosh (1849)]
Aphis Fagi (?) : (C.C. 1850)
Coccos sp. Balfour : (*In*, C.C. 1850, by M'Intosh)
Coccus Fagi Walker (MS.) : (Hardy 1850)
Coccus fagi Walker (1852)
Psylla Fagi (?) : (*In*, R.T.P. 1858, by ?)
[*Psilonia nivea* Fries : (Berkeley and Broome 1859)]
[*Psilonia nivea* Fries : (Berkeley 1860)]
Coccus fagi Walker : (Balfour 1863)
Psilonia nivea Fries : (Berkeley 1865)
Psilonia nivea Fries : (Berkeley 1867)
[*Psilonia nivea* Fries : (Kickx 1867)]
Coccus sp. Ratzeburg (1869)
Adelges fagi (?) : (A.M. 1870)
Psilonia nivea Fries : (Cooke 1871)
? **Chermes fagi** Kaltenbach (1872)
? **Pulvinaria fagi** (Hardy) : Signoret (1873)
? **Chermes fagi** Ratzeburg : (Hartig 1876)
Chermes fagi (?) : (Hartig 1878)
Chermes fagi Kaltenbach : (Hartig 1880)

**The parentheses denote that the generic name is another's. The botanists' custom of appending, in addition, the authority for the new accepted genus is regarded by zoologists as decidedly gauche and it is accordingly omitted with due respect by the present writer.*

[*Psilonia nivea* Fries : (Lambotte 1880)]
Chermes fagi Altum (1881)
? **Pseudococcus** *fagi* (Baerensprung) : Signoret (1876)
Pseudococcus fagi (Baerensprung) : (Douglas 1886)
[**Volutella** *nivea* (Fries) Saccardo (1886)]
Volutella nivea Saccardo : (Cooke 1888)
Cryptococcus *fagi* (Baerensprung) : Douglas (1890)
[*Volutella nivea* (Fries) Saccardo (1892)]
Volutella nivea Saccardo : (Massee 1893)
Adelges fagi (?) : (Massee 1893)
Cryptococcus fagi (Baerensprung) : (Sulc 1896)
? *Schizoneura lanigera* Housmann : (Schröder 1897)
[*Volutella nivea* (Fries) Saccardo : (De Wildeman and Durand 1898)]
Coccus fagi Baerensprung : (Nüsslin 1905)
[*Volutella nivea* (Fries) Saccardo : (Lindau 1909)]
Coccus fagi Baerensprung : (Barbey 1913)
Cryptococcus fagi (Baerensprung) : (Most others subsequent to 1900)

History and Range

In Europe

The first reference to the woolly beech scale, with which the writer is acquainted, is by Fries (1832), in which the "wool" of the insect is described as the "fungus" *Psilonia nivea;* the source of this material is not stated, but, because the same name appears in his "Summa vegetabilium Scandinaviae" (1849), the specimen may be assumed to have come from one of the Scandinavian countries. The Libert (1838) specimens were collected in the Department of Ardennes in the north of France. The first account describing the insect was by Baerensprung (1849) from the Tiergarten in Berlin. Early records from Scotland by M'Intosh (1849, 1850) state that the insect had been present for some years previous at Dalkeith Park, Preston Hall, and Moredun. The first good description was by Hardy (1850) from Scotland; he quotes Walker as writing that the insect had been first observed near London in 1847, and M'Intosh as having observed it 12 years previous (*i.e.* 1838). Other early British notes include that of C. C. (1850), regarding the outbreak in Dalkeith Park; R. T. P. (1858); Berkeley and Broome (1859) in Huntingdonshire, and Berkeley (1860, 1865, 1867); Anon. (1861) at Tunbridge Wells; Balfour (1863) at Tynninghame and Mellerstain; Foggo (1863), who stated that an unnamed insect (which Boodle and Dallimore [1911] are confident is *Cryptococcus fagi)* had been attacking beech trunks for two or three years prior to 1858 and ". . . . is pretty widely spread throughout the country . . . ." (Scotland) (Foggo 1863 : p. 344-5); A. M. (1870); Cooke (1871); Hardy (1885 a, b), reporting the insect from several localities in Berwickshire; Massee (1893); and Miss Ormerod (1898), reporting it at Burton-on-Trent and Newcastle-on-Tyne. Two years later Miss Ormerod (1900) stated that the insect was widely distributed in England, and Newstead (1900) thought that it was probably common throughout Europe wherever beech occurred. Shortly thereafter Wilks reported it from Surrey, Sussex, Kent, and Essex in the southeast of England, and feared that "the Beech is doomed all over the country" (Wilks 1901-1902 : p. 599). In his excellent account of the life history and description of the insect, Newstead (1903) characterized the woolly beech scale as one of the commonest native coccids, generally and very widely distributed throughout the British Isles, and mentioned specifically 24 counties or regions in various parts of England, Scotland, Wales, and one in Ireland (Dublin) where it was known to occur. In the same year Carpenter (1903) reported it from the Botanic

Gardens of the University of Dublin, and from Rostrevor in Ireland. Subsequent substantiating notes for the British Isles include those of Brotherston (1904), Theobald (1904, 1905, 1906, 1907, 1908, 1909, 1911, 1912, 1913), Boulger (1907), Gillanders (1908), MacDougall (1908), Webster (1908), the Board of Agriculture (Anon. 1910, 1911), Green (1915), Warburton (1918, 1922), and the Forestry Commission (1926). Worthy of special comment are the detailed observations of Boodle and Dallimore (1911 : p. 339), and their conclusion: "There can be no doubt that the Coccus is widely distributed about the country at the present time, as it has been for the last 50 years. It is also equally evident that it has, on the whole, increased in quantity during the last 15 years . . . ."

Meanwhile, in Germany Hartig had been impressed by the abundance of the insect at Eberswalde (Prussia) since 1867, and in 1880 reported it as quite general throughout Germany. Altum (1881) noted its especial abundance in the western provinces, notably Westfalen. Judeich and Nitsche (1895), in their eighth edition of Ratzeburg's textbook, stated that the insect occurred throughout central Europe and England. Subsequent notes or papers by Schröder (1897), Reh (1903), Lindau (1909), Bertelsmann (1913 a, b), D. in E. (1914), Rhumbler (1914 a, b, 1915, 1922, 1931), Eckstein (1920), Sachtleben and Pape (1922), and others, indicate that the insect is still widespread in Germany and attracting the attention of entomologists and foresters.

For the remainder of Europe, it has been reported from Belgium by Kickx (1867) in Flanders, Lambotte (1880), De Wildeman and Durand (1898), Huberty (according to Judeich and Nitsche 1895), and in the Forêt de Soignes by the Great Britain Board of Agriculture (Anon. 1910), and by Vayssière (1926), who also examined many specimens in the Limbourg belge. French records include those of Libert (1838) from Ardennes; Marchal (1908), who found the insect in small quantity on old beeches in the Forêt de Montmorency near St. Leu (Seine-et-Oise) but believed it to be rather rare in the environs of Paris; Barbey (1913); P. L. (1916); and Vayssière (1926), who stated that Marchal in 1907, and P. Lesne had also seen the insect in the Bois de Meudon, but who himself had never found it in the magnificent beechwoods of Normandie, nor in the Forêt de Rambouillet, nor in the beech stands of the French Alps. It was reported from Switzerland by Marchal (1908) at Lausanne, and (in addition to other countries) by MacGillivray (1921). It was reported from Czechoslovakia as occurring in several localities in Bohemia (Sulc 1896); from Holland as spreading slowly (Anon. 1921); from southern Sweden as occurring comparatively rarely (Trägårdh 1921); and from Denmark (in addition to other countries) by Graham (1927), although the present writer has discovered no specific references to its occurrence there.

Concerning the European range of *Cryptococcus fagi*, Vayssière (1926) pointed out that although beech occurs in all of the temperate portions of Europe, Asia, America, and Australia, the woolly beech scale has been re-

ported thus far only in the cooler parts of the European beech range. He regards the insect as a northern coccid, which appears to be limited in its southward distribution in Europe by latitude 49 degrees north. Although in North America the insect already exists as far south as latitude 42 degrees north, it is quite possible that this is permitted by the cooler climate of the western shores of the Atlantic and that future distribution of the insect into the beech stands of the central and southern Appalachian uplands may be limited by their warmer climate.

In North America

In America there are no records at hand prior to 1914, other than its recognition as a European insect by Cockerell (1899) and Fernald (1903). In 1914 Braucher published the following correspondence: (1) from a letter regarding this insect, written October 2, 1913, by L. G. Vair: "The trouble is noticeable all through the woods in the vicinity of Halifax, N.S. . . . ."; (2) from a letter written November 6, 1913, by Dr. L. O. Howard: "I have referred this material to Mr. Sanford, who is of the opinion that it is the European felt scale *(Cryptococcus fagi* Baerens.). So far as I am aware, this is the first report of the occurrence of this coccid in North America . . . . Doubtless it has been imported on European stock, and measures should be taken to prevent its becoming widely distributed" (Braucher 1914 : p. 14). Shortly after the appearance of Braucher's note, Hewitt (1914), the Dominion Entomologist for Canada at that time, published a note correcting Braucher's impression that the insect had been found for the first time in America. He reported having received specimens in 1911 from Bedford and Halifax, that he had found the insect on both ornamental and forest beech in the vicinity of Halifax where it had apparently existed for a number of years, and that the superintendent of the Public Gardens in Halifax had known of the presence of the insect for at least 20 years, where he had been spraying the purple-leaved variety of beech. He was of the opinion that the insect might have been introduced into Canada a number of years previously on ornamental beeches from Europe. It appears from these two accounts that the woolly beech scale was present in Halifax probably as early as 1890, that it occurred on imported specimens of the European beech *(Fagus sylvatica* L.) at the outset and may well have been introduced with such specimens, and that by 1914 it had become generally established in the stands of American beech *(Fagus grandifolia* Ehrh.) in the forests about Halifax.

In the following years the insect apparently spread steadily from its assumed point of origin at Halifax. By 1926 Hutchings reported it as established not only in Nova Scotia but also in Prince Edward Island; and Motherwell (1926) mentioned it as established in parts of the Maritime Provinces. By this time reports of the injury and death which attended infestation were becoming frequent and widespread, with the result that a preliminary investigation was made by the Dominion Entomological Branch and the Nova Scotia Department of Lands and Forests, which showed the insect to be present in every county in the province, but not yet in the adjoining province

of New Brunswick (Graham 1927). In 1929 Gorham observed the insect to be abundant in stands of beech in Prince County, Prince Edward Island, and late the same year Gorham, Walker, and Simpson (1929) reported it for the first time in the part of New Brunswick which adjoins Nova Scotia, stating that it had been first noted in 1927 near Dorchester in Westmoreland County and in Albert County, and that at the time of writing (1929) it was present in most of the beech areas of both counties. Subsequent notes on its occurrence in these areas were made by Swaine (1930), Ehrlich (1931, 1932 b), Balch (1932), and Balch and Simpson (1933). Observations were continued by members of the Federal Entomological Branch Laboratory (Fredericton, N.B.), with the result that by the autumn of 1932 the insect was found in a number of beech stands in the southern part of New Brunswick, not only in Westmoreland and Albert Counties, but also in Queens and Charlotte Counties (Fig. 1) (Ehrlich 1933 b).

In the United States the woolly beech scale was apparently first recognized in November, 1929, upon its discovery in Boston by the present writer (Ehrlich 1932 a) on ornamental beech in the Arnold Arboretum and in certain of the park lands. Both the appearance of the infestation and the word of a park employee indicated that the attack was about 10 years old in certain places. Further search with the assistance of the Boston Park Department lead to the discovery of infestation in a number of points throughout the Metropolitan District. When in the spring of 1931 the United States Bureau of Entomology was informed of the presence of this insect, through chancing on a control experiment being prosecuted under the direction of the writer in the Middlesex Fells, members of the staff of the Melrose Highlands Laboratory joined in the search. Several additional outbreaks were discovered, and by autumn of 1932 infestations were known to exist in Boston (Suffolk County), Brookline (Norfolk County), and the neighboring towns of Gloucester, Essex, Manchester, Beverly (Essex County), Stoneham, Cambridge, Belmont, Watertown, Newton (Middlesex County), and Milton (Norfolk County), but none beyond, although search was made by members of the staff of the Melrose Highlands Laboratory in many areas on all sides of Boston as well as points in Rhode Island and New Hampshire. During 1931 a young outbreak was found in the town of Liberty, Maine, by members of the Melrose Highlands Laboratory. Further scouting in Maine by the State Entomologist during 1932 lead to the discovery of additional outbreaks in surrounding towns and an older infestation in eastern Maine adjacent to the New Brunswick border. By the winter of 1932-1933 the insect had been found in the following Maine towns: Robinston, Perry, Baring, Meddybemps, Charlotte, Pembroke, Dennysville (Robinson), Northfield, and Whitneyville in Washington County (eastern Maine); Montville, Palermo, and Liberty in Waldo County, Somerville in Lincoln County, and Washington in Knox County (south central Maine) (Peirson 1932, 1933 a, b).

The entire known American range is indicated approximately on the sketch map (Fig. 1). In addition to the note reporting the first discovery of

the insect in the United States (Ehrlich 1932 a), other notices dealing with outbreaks in New England were published by Collins (1931, 1932), Schaffner (1931), Peirson (1932, 1933 a, b), Hayden (1932), Beattie (1933), Felt (1933), and Ehrlich (1933 a, b).

It is not known how or when the insect made its first appearance in the United States. That it was introduced is most probable. It may have come to Massachusetts from the Maritime Provinces, with which there is much intercourse both by land and by sea, either on nursery stock or as bits of wool containing eggs and crawlers, clinging to anything and being disseminated by the wind on arrival. Or it may have been introduced directly from Europe on stock of *Fagus sylvatica*, which is commonly planted in parks and estates throughout the now infested area. So far as the writer is aware, there is no direct evidence in support of either alternative. The outbreak in eastern Maine may well be a spreading of the infestation in the Maritime Provinces. Whether the insect now occurs elsewhere, other than in south central Maine, is not yet known; but if not, it is difficult to understand how or why this particular area, which is sparsely settled and not traversed by trunk railroads or important highways, should have been the only point attacked.

Description

Although *Cryptococcus fagi* was first reported as an insect by Baerensprung in 1849, and partially described by Hardy in 1850, it was not until 1886 that Douglas published a detailed description. Other careful observations were reported by Sulc (1896) and Newstead (1903). Certain of the early descriptions are included in the present account for their historical interest, beginning with Fries' (1832) "*Psilonia nivea*," which is believed to be the woolly secretion of this insect.

"*P. nivea*, caespitibus compactis laneis candidis, floccis ramosis intorto-intricatis.

"Caespites erumpentes, rotundi, 1—2 lin. lati, lineam alti, compacti, licet flocci omnino discreti sint, rotundato-irregulares, confluentes. Flocci crassiusculi, non pellucidi, sed transparentes tantum, ramis patentibus instructi, contigui, intorte et implexi, apice attenuati. Sporidia (potius *Gonidia*) minuta, globosa, tarde diffluentia, sed subinde immixta vidi sporidia cylindrica, curva, ut ad Menisporas pertineret. *E rimis corticis Fagi erumpit hieme.*" (Fries 1832 : p. 450.)

The "sporidia" which Fries saw in his surface examination of the material which he thought to be erumpent from the sub-phellar bark do not, in the present writer's judgment, cast doubt on the belief that the material was in truth the "wool" of *Cryptococcus fagi;* the spores of any one of a number of Mucedinaceous fungi may well have been present and been misinterpreted as belonging to the material under observation.

The first formal description of the insect is the following brief note by Baerensprung (1849 : p. 174):

"♂ ?

"♀ lutea, ovata, abdominis apice hirsuta; capite minuto, antennis brevibus crassis. Long. $\frac{3}{4}$ lin." This is supplemented with notes summarized as follows. Females enclosed in a thick weft, produced especially by the hind part of the thick, soft, sulphur-yellow animals. Antennae short and thick, next to the black eye-spots. The short legs almost completely retracted into the fleshy body. Larvae of same elliptical shape, with two red eyepoints, five-membered antennae with bristles at their ends. Last member of hind leg provided with two pairs of papillae, a smaller inner one and a larger outer one, with a few bristles between.

Walker's (1852) description of his proposed new species, *Coccus fagi*, was quite as laconic:

"Flava, elliptica, albo-farinosa.

"Yellow, elliptical, covered with white powder. Length of the body 2 lines. England." The "2 lines" is obviously an error since a line equals $\frac{1}{12}$ inch, and the largest females never attain anything like such size.

The "woolly" secretion of the insect was subjected to chemical analysis and reported to be a new wax, very close to China wax, having a melting point of about 80° C., and the following composition: C, 81.39; H, 13.58; and O, 5.03% (Anon. 1884). Various tests on this material were reported by Hardy (1850).

The first careful description of the insect was given by Douglas (1886). Its main features are summarized in Tables VII and IX. A decade later it was reported (Judeich and Nitsche 1895) that recent observations by Nitsche showed the description of the legs of the adult as given by Baerensprung and by Douglas to be in error; Nitsche stated that the adult female does not have reduced legs embedded in the body, but has no legs at all, only vestiges marking their earlier position. More recent observations have shown that Nitsche was correct. Sulc (1896) redescribed the insect, giving notes on the diagnostically important anal characters (see Tables VIII and IX), and publishing the first accurate drawings. In his "Monograph of the Coccidae of the British Isles," Newstead (1903) gave an excellent illustrated account of *Cryptococcus fagi*, the salient points of which are included in Tables VII, VIII, and IX. When Rhumbler (1915) reported his studies of this insect, he gave measurements

TABLE VII

COMPARISON OF DESCRIPTIONS OF EGG, *Cryptococcus fagi*

	Douglas	Judeich and Nitsche	Newstead
Color	Pale yellow	—	Lemon-yellow
Shape	Oval	—	—
Size	Large	Approx. 0.6 mm.	Very large in proportion to size of insect
Number laid at sitting	7–8	—	4 or 5 in strings attached end to end

of the first two nymphal forms and the adult, which are presented in Tables VIII and IX.

Illustrations of the insect appear in Fig. 10. Hartig's (1880) sketch of the crawler (Fig. 10 A), although lacking in detail, gives an excellent general impression. A more detailed original camera-lucida drawing (Fig. 10 B) of dorsal (right half) and ventral (left half) aspects shows the position of spines and hairs, and the structure of legs and antennae. More highly magnified original drawings from ventral and dorsal aspects of the anal

TABLE VIII

COMPARISON OF DESCRIPTIONS OF CRAWLER, *Cryptococcus fagi*

	Sulc	Newstead	Rhumbler Form I	Rhumbler Form II
Color	Reddish yellow	Lemon-yellow	—	—
Shape	Elliptical	Elongate ovate	Slim, turnip-shaped	Thicker set
Size	—	—	0.24–0.33 mm.	0.35–0.38 mm.
Body length / Leg length	—	—	3/1	4/1
Eyes	Distinct, reddish brown	Large	—	—
Antennae	5-segmented 2nd>basal, 5th,>3rd, 4th; 2 small hairs on each segment; 2 short obtuse and 2 long fine hairs on 5th segment	5-segmented 2>5>1>3 and 4	5-segmented	5-segmented
Rostrum	Mentum dimerous, with hairs	Large, mentum uniarticulate	—	—
Stylets	—	Exceeding length of body	—	—
Legs	Strong; coxa large; trochanter wedge-shaped, with rather long hair; femur massive, as long as tibia and tarsus together; 2 pairs digitules on tarsus; a hair in incision proximad of inferior pair; terminated distally by simple untoothed claw equal in length to tarsus	Short; stout; tibiotarsal segments short and equally divided; claw long; digitules to claw and tarsi ordinary	Present	Present
Abdomen	Distinctly segmented; 2 hairs on side of each segment	—	—	—
Anal segment	2 pairs of tubercles with strong conical spines on apex; 1 long bristle on base of each single inferior tubercle (ventrally); inwards from it a small simple hair	Slightly truncate, lobes faintly projecting but extremely minute, each with single spine; similar small spiniferous lobule on ventral surface; single long slender hair arising from base of each lobe on ventral surface	—	—
Anus	Orifice oval, with superior pair and inferior pair of hairs	—	—	—

TABLE IX

COMPARISON OF DESCRIPTIONS OF ADULT FEMALE, *Cryptococcus fagi*

	Douglas	Sulc	Newstead
Color	Sulphur-yellow	Canary-yellow	Lemon-yellow
Form	Short rounded-oval, nearly circular, very convex above and below, almost globose	Elliptical, almost sub-circular	Hemispherical, convex above, comparatively flat beneath, anal extremity slightly curved ventrally
Length	Barely ½ line long	0.44 × 0.47 mm.	0.75–1.00 mm. (0.5–0.8 mm. : Rhumbler)
Hairs, spines	Finest pubescence above, no projections at sides or end except pale setaceous hairs on end	—	Minute spines numerous
Segments	All determinable, the junction of their ventral and dorsal rings forming a continuous thickening	Segmentation of pre-abdominal part indiscernible	Segmentation faintly indicated
Eyes	2, on ventral anterior margin of head, blackish, angular, rounded in front, extending obliquely inward and downward to long fine point	Simple, reddish brown, on anterior periphery	—
Rostrum	Short, appressed, covered, with free end turned at right angle, brown, tubular	Mentum dimerous, with 2 long and 6 short hairs	Reddish brown, mentum uniarticulate
Stylets	Extremely fine blackish "seta," 3 times length of body	—	Nearly 2× length of body
Antennae	Short, thick, apparently of 3 segments only, concolorous	Atrophied, only a stump with 2–4 long hairs	Reddish brown, rudimentary, of 3 segments, generally 2 short stout spines on 2nd segment, shorter spine on 1st segment
Legs	Short, embedded in the fat body, concolorous, difficult to see	1st and 2nd pairs absent, only saccate stumps of 3rd pair present	Reddish brown, 1st and 2nd pairs obsolete, 3rd pair represented by minute tuberculate projections
Wax glands	—	On whole surface of body without order, especially on abdomen	Numerous, minute tubular and large circular, latter forming distinct bands on abdominal segments above
Anus	—	Elliptical, with thickened margin, 2 hairs anteriorly and 2 posteriorly, on each side 3 strong spines	Anal lobes obsolete, position indicated by single large spine and short stiff hair; 2 similar hairs anterior to anal orifice on ventral surface; anal orifice with 4 spines in 2 pairs, 1 anterior, 1 posterior; between anterior are several circular glands; small inner chitinous ring

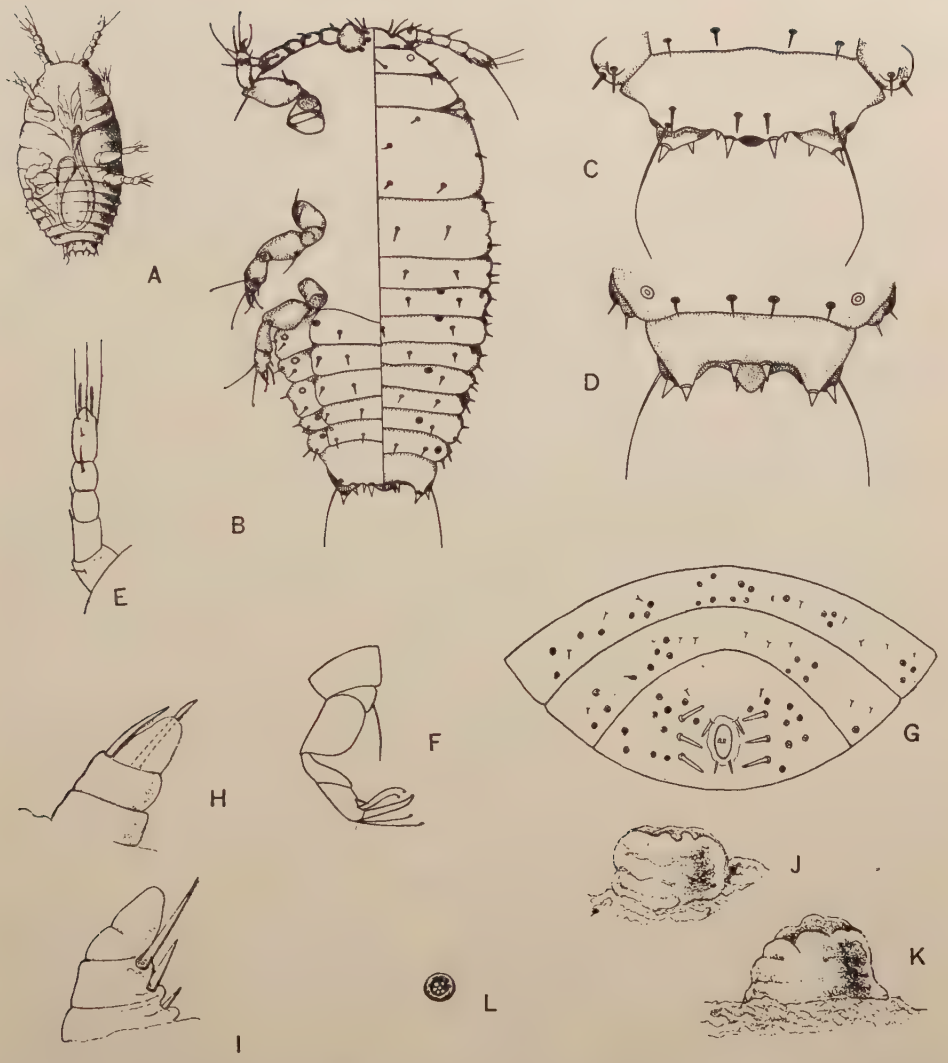

FIG. 10. *A. Crawler of Cryptococcus fagi (from Hartig 1880). B. Crawler; right half, dorsal; left half, ventral (original). C. Anal region of crawler, ventral aspect (original). D. Anal region of crawler, dorsal aspect (original). E. Antenna of crawler (from Sulc 1896). F. Leg of crawler (from Sulc). G. Anal region of adult (from Sulc). H. I. Vestigial antennae of adult (from Newstead 1903). J. K. Vestiges of third pair of legs of adult (from Newstead). L. Wax plate of adult (from Sulc).*

region of the crawler (Fig. 10 C and D) show the exact locations of the diagnostically important anal spines, hairs, and bristles. Sulc's drawings of antenna and leg appear in Figs. 10 E and F, respectively. The anal region of the adult, as figured by Sulc (Fig. 10 G) is somewhat diagrammatic but correct in the number and location of spines. The vestigial antennae of the adult and the vestiges of the third pair of legs (from Newstead) appear in Fig. 10 H, I, and J, K, respectively. A wax plate from Sulc is represented in Fig. 10 L.

In brief, this insect is a typical coccid, with oviparity, motile first-instar nymph, degenerate parthenogenetic adult female, and male unknown. The "scale" of this species consists of a loose mass of curled white threads which form the ovisac and a fluffy wool-like canopy over the colony. The diagnostic characters of the first instar nymph or crawler are two pairs of setiferous anal lobes, the ventral pair bearing each a long slender bristle, two pairs of anal spines, three pairs of strong typical legs, and five-segmented antennae. The distinguishing features of the adult female are vestigial three-segmented antennae, absence of the first two pairs of legs and tuberculate vestiges of the third pair, two trimerous sets of lateral spines flanking the anus, and an anal ring bearing an anterior and a posterior pair of spines.

Life History and Habits

Scattered notes on the life history of *Cryptococcus fagi* occur in the early literature. Baerensprung (1849) in Germany reported finding eggs and nymphs in December, but no adults. Kaltenbach (1872) found eggs and dead females in winter, nymphs in spring, and again eggs and nymphs in summer. Kessler (1884) reported eggs in winter, eggs and nymphs in spring, eggs, nymphs, and pregnant females in summer. Douglas (1886) in England observed eggs and crawlers in winter, females at the end of May, ovipositing females, eggs, and nymphs in the middle of July. Nitsche (1895) in Germany found eggs and crawlers in winter, eggs and nymphs in summer, and nymphs in autumn. Miss Ormerod (1900) stated that in England eggs were laid in June and that she found crawlers on July 4. Newstead (1900) stated that the crawlers hatch in September. The first careful observations on the life history of this insect were made in England by Newstead (1903). His account follows.

"The eggs are laid at the beginning of July, and the larvae hatch in the autumn, and apparently also in the spring. On hatching from the egg the majority of the larvae work their way under the bodies of their dying or dead parents, taking up their positions by preference in the deepest parts of the fissures in the bark, where they remain for the rest of their lives, pumping up the juices of the tree. Each individual protects or covers its body with secretion, which adds to that already secreted above them by their parents; thus the secretion gradually thickens and spreads over the tree trunk, eventually forming a more or less continuous mass, often attaining a great thickness . . . . In such masses one finds the remains of many generations of females. When an insect takes up a separate abode the secretion forms a complete and approximately round sac, such sacs being commonly met with on newly infested trees, or on the branches just above the trunk of a badly infested tree. It is on the trunks of the very old trees (50 to 100 years) that the insects are found in the greatest numbers, and they probably represent the survivors of many generations which have lived, cycle upon cycle, on the same tree. The larvae do not appear to be of a wandering habit, and comparatively few seek the fresh untenanted bark; the main branches, as a rule, are not attacked to the same extent as the main trunk. Those larvae which

wander over the trees are liable to be borne away by the wind or by birds to other trees, and this is probably the means by which fresh colonies are started." (Newstead 1903 : p. 219-220).

Simultaneously, Reh (1903) reported observations on the life history of this insect in Germany. His notes include winter observations of crawlers in November, old dead females and eggs in December, and nymphs in February; spring observations of nymphs on April 8, and young females on April 14, and May 21; summer observations of nymphs and females in June and in August; and autumn observations of old females, eggs, and young nymphs in September, and dead females and nymphs in October.

The next detailed studies to be reported were made in Germany by Rhumbler (1914 a, b, 1915), some of whose observations follow. The insect hibernates on the bark as a wool-clothed nymph, either as Form I, in which case transformation to Form II takes place in February, or as Form II. Between April and July the Form II nymphs moult and develop into adults. Oviposition begins in the first week of June and continues to the end of October, the adults remaining fixed throughout this period in their ovisacs composed of the curly threaded wax secretion which covers them with a fluffy white down; the act is periodic, each female laying several batches of eggs, each batch comprising not more than seven or eight eggs. The duration of the incubation period varies inversely with temperature; at the relatively uniform temperatures of the laboratory, eggs under observation hatched in 25 or 26 days during August and September; out of doors, 45 to 50 days were required during September and October. The Form I nymphs are active crawlers; although certain individuals never leave the ovisac but insert their stylets into the bark and begin feeding in the maternal nest, the majority roam over the bark, primarily upwards and towards the light, probing the bark here and there as they wander. The speed and skill of their locomotion increase with temperature; they have been observed on a warm afternoon to travel a vertical distance in the sunshine of more than two metres. Eventually they settle down, insert their proboscal setae (stylets) into the bark, and remain fixed in position thereafter. Secretion of "wool" begins rarely while they are still crawling, usually promptly after settling, and occasionally not until four weeks later. These crawlers then overwinter *in situ*, some of them changing first into Form II nymphs. The mothers die in the late autumn. The life cycle is thus annual.

In a subsequent account Rhumbler (1922) contributed the following additions or changes. The Form I nymphs occur from July to December and are present abundantly in September and October. Their crawling is interrupted at night and while the bark is wet. Following cessation of crawling, the change from Form I to Form II is one of growing and compacting of the body which retains the now useless and relatively small legs. The Form II nymphs moult between April and July and metamorphose into elongate, legless, second-instar nymphs. These nymphs moult once more and develop into egg-laying parthenogenetic females. When the latter die in late autumn

they shrink, darken in color, and are frequently inhabited by a species of *Cladosporium* which converts the outer wool into a brown weft covering the fresh white wool and younger generation beneath.

The essential points in the foregoing account were repeated by Eckstein (1920) and Reichling (1920) in Germany and by Anon. (1921) in Holland. Trägårdh (1921) found that in southern Sweden eggs occur in August and the crawlers appear later in the autumn.

In Nova Scotia Graham (1927) found "the young scale stage" on June 17, 1926; this changed to the adult during the remainder of June and all of July. Oviposition was first observed on July 22 and hatching on August 10, continuing well into September. The present writer's summer observations in Nova Scotia and southern New Brunswick show that by June the adult stage has been reached and that pregnancy is visible by the latter part of the month. The date of first oviposition varies from year to year, but occurs in the first or second week of July. Hatching may begin in a few cases by the end of July but is not common until about August 10. In Boston, oviposition and hatching begin somewhat earlier than in the Maritime Provinces; the Form I nymphs cease crawling at approximately the middle of September and by October all crawlers still alive have settled in crevices and begun secreting "wool." The species overwinters as Form I and Form II nymphs; eggs which have not hatched by September are lost.

The foregoing notes on the life cycle of *Cryptococcus fagi* may be summarized in tabular form, as in Table X.

TABLE X

SUMMARY OF NOTES ON SALIENT POINTS IN THE LIFE CYCLE OF *Cryptococcus fagi*

	Germany Holland	England	Sweden	Maritime Prov. New England
Overwinters as	Eggs and nymphs	Eggs and nymphs	?	Nymphs
Oviposition begins	Early June	June (Ormerod) Early July (Newstead) Middle of July (Douglas)	August	Early July
Hatching begins	Early July (Rhumbler) September (Reh)	September and spring (Newstead) Early July (Ormerod)	Autumn	Early August
Crawling ceases	During October	?	?	During September

Oviposition was observed by Kessler (1884) to consist in the laying at one sitting of four or five eggs in horizontal or vertical strings, followed by the addition of another egg to the string on the next day.

Although Rhumbler's statement that the larvae crawl upwards predominantly is correct, this is far from invariable; Rhumbler himself reported

catching them in great numbers on glue-coated slides placed on the forest floor; however, it is probable that many of these fell or were washed or blown from the trees. The numbers that crawl during favorable weather are enormous; fresh bands of tar painted around trunks of beech in the forenoon were bordered by afternoon with a quantity of larvae so great that a fine yellow margin could be detected at a distance of several yards from the tree; and this margin was almost as dense on the upper side of the band as on the lower, indicating that with ample warmth and sunshine the orientation is not rigid. Although great numbers of the wandering larvae are blown away, washed down by rain, or killed by exposure, many eventually settle in sheltered places suitable for feeding; such places include lenticular crevices and other cracks or wounds, especially on the more shaded and lee side of the trunk, abaxillary angles of the lower branches, the undersides of branches, and areas under thalli of mosses and foliose lichens epiphytic on the bark.

All stages of the species feed by forcibly inserting their slender powerful stylets (modified maxillae and mandibles) into the bark and pumping and sucking in the manner characteristic of plant-inhabiting insects with sucking mouthparts. The strength with which the stylets are directed is attested to by the fact that when the observer forcibly raises an individual so that the stylets are partly withdrawn from the bark, the insect is frequently seen to wave its body in the air, pivoted only on the stylets. Their mobility can be seen by raising an individual from the bark, turning it so that its back rests on the substratum, and watching the wavings and bendings of the raised stylets; this flexibility is also indicated by the often tortuous courses and bifurcations of the stylet sheaths when observed in sections of the bark, which show that in the course of prolonged feeding in one area on the bark the insect probes in all directions into the tissues within reach of its stylets, bending them at any point in their length, as demanded by the tissues encountered.

Dissemination and Distribution

Local spread of *Cryptococcus fagi* takes place during the period in its life cycle when it is capable of becoming established on a fresh substratum, that is, as eggs and as Form I nymphs; older stages are transported by various agencies but, being legless, are unable to seek favorable nesting places and die of exposure and starvation. Since there are no winged forms, dissemination is effected by the wandering of the crawlers (Form I nymphs) and by agencies which carry eggs and nymphs.

The crawlers are active and have been found capable of travelling a distance of two metres on a sunny afternoon (Rhumbler 1915). Although Newstead believed that "the larvae do not appear to be of a wandering habit, and comparatively few seek the fresh untenanted bark" (1903 : p. 320), this is hardly borne out by the observations of Rhumbler and of the present writer. The numbers on the move during a favorable day are enormous in a well infested beech stand; Eckstein (1920) counted over two million individuals on a single square metre of bark surface. Crawling is the principal means

of spread on individual trees and to a less extent to adjacent trees. The latter is indicated by the fact that Rhumbler (1915) regularly caught crawlers on glue-coated slides placed on the ground (although it is not unlikely that some of those caught had been blown from infested trunks), and by the present writer's repeated observation that in a recently infested stand the first attacks on nearby trees usually begin at the butt and proceed upwards. Rhumbler himself believed crawling to be of no importance whatever in initiating attacks on uninfested trees.

The leading agencies which have been assumed to carry eggs and nymphs are wind and birds. Both were suggested by Newstead (1903) and Bertelsmann (1913 a); Rhumbler (1915) suspended glue-covered slides in the air and caught great numbers of nymphs, far more than on the terrestrial slides. Similar tests were made in Nova Scotia by Graham (1927), who caught eggs and naked nymphs at maximum distances of over 300 yards from their source. The present writer also frequently trapped naked nymphs on slides set to catch fungal spores. Many authors have assumed that birds carry the eggs and nymphs and in this way play a role in local dissemination and in long-range distribution. Newstead (1903) thought that birds were probably a means of starting fresh colonies; Bertelsmann (1913 a) listed not only birds seeking insects on the trunk, especially woodpeckers, tree creepers, and nut peckers (?), but also squirrels; Reichling (1920) believed that squirrels, woodpeckers, and titmice were not insignificant carriers; Eckstein (1920) mentioned squirrels, woodpeckers, nuthatches, and tree creepers as possible minor carriers. Mammals such as porcupines, moose, deer, and bear, whose gnawings are occasionally encountered on beech in the Maritime Provinces, may also act as local agents of dispersal. So far as the present writer is aware, no critical observations or experiments devised to test these assumptions have been performed.

The means of long-range dissemination can only be conjectured. Transportation of infested beech stock is doubtless occasionally a means and was probably the source of the first Nova Scotian outbreaks. Wind can undoubtedly carry eggs and nymphs for many miles and lead to the establishment of infestations in distant areas; a limitation would be the vitality of the insect, regarding which nothing definite is known; wind seems the only likely means of bringing inoculum to so isolated and distant an area as that in south central Maine. Man and his vehicles of transportation may also carry bits of wool or naked eggs and nymphs, and scatter them occasionally on suitable substrata. In short, effective spread of the insect takes place by means of eggs and Form I nymphs, which, in most countries other than England where the insect has been studied, is during the months of June to November. Local dissemination is by crawling and wind, and possibly by birds and mammals. The means of long-range distribution are not known with certainty, but may include wind, transportation of nursery stock, and chance carriage on ships, trains, and automobiles.

Factors Influencing Infestation

It is characteristic of infestations of *Cryptococcus fagi* that when they become established in a forest area, scarcely a beech remains free of attack, practically every tree harboring at least a few of the insects, irrespective of size and vigor of the tree, of proportion of beech to other species in the stand, of local nature of the stand, and of physiographic factors. In spite of this total infestation, differences in severity of the infestation are regularly apparent, varying with a number of conditions. Those which have been suspected of influencing severity are *(a)* the tree factors—health and size of the tree, nature of the bark, amount of lichens and mosses, position in stand, and those determining which side of the trunk is most heavily infested; *(b)* the stand factors—density of stand, position of stand, and soil; *(c)* climate.

Tree factors

Health of tree. As early as 1849 M'Intosh pointed out that old and "sickly" trees are most heavily infested; but apparently his observations were none too extensive, since Balfour (1863) claimed that only healthy trees are attacked, a view also expressed by German foresters (Piller, in Hartig 1880; Bertelsmann 1913 a). Webster (1908) believed that the severity of infestation is independent of the health of the tree. Rhumbler (1914) advanced the opinion that in an area already exposed to infestation, a marked outbreak consists merely in an increase of the infestation due to injury or disease of the more heavily attacked trees; in support of this view he pointed to the generally recognized fact that certain obviously healthy trees remain free of the insect while adjacent individuals support an increasingly dense coating. A few years later Rhumbler (1922) stated that a slime-flux infection of unknown origin is the initial disturber of the healthy tree and that its activity favors a heavy infestation by the woolly beech scale. The present writer's observations lead to no certain conviction that the original health or vigor of the tree play any part in the building up of a heavy infestation. In both the Maritime Provinces and New England slime-flux or other infections associated with this disease and subsequent *Scolytid*-beetle invasions develop only after *Cryptococcus* has been present for some time. Possible decreases in the vigor of the tree due to partial girdling by porcupines and extensive leaf injury due to *Tortricid* larvae have no appreciable influence on infestation.

Both Reichling (1920) and Eckstein (1920) pointed out that healthy and vigorous trees which are not infected subsequent to *Cryptococcus* attack frequently lose their insect inhabitants and remain uninfested for long periods. This condition has been observed in several places by the present writer; it is believed to be the result of an enormous regional increase in *Cryptococcus* nymphs due to favorable climatic conditions, and the consequent infestation of trees which under climatic conditions less propitious to the insect could not offer adequate shelter; if such trees remain uninfected, a season unfavorable to the insect causes the death of those which are not adequately protected.

Size of tree. Whether or not a beech becomes infested is not influenced by size or age of tree. This has been recognized from the start. M'Intosh (1849) reported the insect on all trees observed over 11 years old. Ricker (Hartig 1880) stated that infestation is independent of crown class. Boulger (1907), Webster (1908), Bertelsmann (1913 a), Eckstein (1920), and Reichling (1920) reported trees of all ages infested; Rhumbler (1915) examined systematically over 1000 beeches over two centimetres ($\frac{3}{4}$ inch) in diameter in two districts of Münden and found not a single tree uninfested. The present writer's general observations in the Maritime Provinces and New England, and systematic records of more than 1000 tagged trees in permanent sample plots examined three times and of more than 4000 beech in temporary sample plots substantiate the foregoing statements. The insect was commonly found in infested stands on saplings under 4.5 ft. in height. The amount of infestation on individual trees was found, however, to vary considerably with size of tree. Small saplings usually harbor a very few small colonies, and trees of small diameter rarely support as dense a mass of insects as the larger individuals; but trees over approximately 16 inches in diameter are frequently less heavily infested than smaller ones. The writer believes these differences to be due to other factors associated with size of tree, such as nature of bark, and abundance of lichens and mosses.

Nature of bark. The characteristics of the bark which may be presumed to affect the size and number of colonies are of two kinds—those limiting the ability of the insect to puncture the bark and gain nourishment, and those determining its ability to survive unfavorable meteorological conditions. The former include depth of the cork layer, proportion of sclerenchyma to parenchyma in the tissues within reach of the stylets, hardness as influenced by moisture, nature of the shelter afforded by lenticular crevices, foliose lichens, and mosses. The effect of proportion of sclerenchyma to parenchyma has been studied for certain other plant-sucking insects, but has not yet been investigated for *Cryptococcus fagi*. Hartig (1876, 1878) pointed out that *Cryptococcus* colonies develop most abundantly on areas of young callus bark where the cork layer is thin (and where there is as yet little sclerenchyma), such as on the edges of cankers produced by frost and by *Nectria ditissima*. Rhumbler (1915) believed the nature of the bark to be a minor factor, but that the insect avoids exceedingly soft (?) and corky bark, and favors thin secondary bark such as callus over cankers and wounds produced by the antlers of deer; neither absolute nor relative thickness of bark was believed to affect infestation. Bertelsmann (1913 a) observed attack to be light on smooth, hard, shiny steel-gray bark and heavy on soft bark; Eckstein (1920), on the contrary, claimed that the latter type is more heavily attacked, while Reichling (1920) believed that soft bark is favored. Bertelsmann pointed out that bark while moist is softer than when it dries and that therefore bark in moister situations is more heavily infested.

Since the smooth unbroken bark offers no shelter to the insect against driving rains, strong winds, and hot sun, the insects are usually more numerous

in places where some protection against these elements exists. Wounds, cracks, lenticular crevices, mosses, and foliose lichens all provide such shelter. In addition, all retain moisture following rains for longer periods than the smooth exposed surfaces of the bark and therefore maintain the bark in a condition better suited to penetration by the stylets. The role of lichens was recognized by Hartig (1876), by Bertelsmann (1913 a) who pointed out that the insects avoid trees from which *Limax arborum* has removed the lichens and *Protococcus pluvialis*, and by Reichling (1920). The present writer found the bark beneath lichens which abound on beech in the Maritime Provinces (especially species of *Parmelia*) to be the first attacked; in fact, many newly infested trees which showed little or no sign of the insect at first glance were found to harbor considerable numbers under the lichen thalli. This condition was most pronounced in somewhat open stands where the exposed bark offered none too favorable a substratum.

Side of tree. It has often been thought that certain sides of the trunk should be more heavily infested than others. Kaltenbach (1872) detected no differences in infestation on the various sides; Ricker (Hartig 1880) saw no differences within the stand but observed infestation at the edges of stands on the eastern side only, which was to the lee of prevailing winds; similarly Boulger (1907), the Forestry Commission (1926), and Graham (1927) found infestation heaviest on the sheltered side of exposed trees; Bertelsmann (1913 a) found that in his district the east and north sides were preferred, and attributed this to more lichens, greater moisture, and the lee of prevailing winds. The present writer took systematic notes in permanent sample plots on the relative intensity of infestation on different sides of the tree and found no consistent trend; but observations showed that the sheltered side, as determined by local conditions, is always the most heavily attacked.

Stand Factors

Soil. The relation of quality, tilth, and depth of soil to ability of the tree to withstand attack has not been studied. Hartig (1880) believed that the injury caused by the insect is probably greater on poor soils, but this is more a question of resistance of the tree to attack than of intensity of attack. In this connection Boodle and Dallimore (1911) quoted a letter in which Brotherston stated that the nature of the soil has no influence on resistance of the tree to attack, those growing in pure sand being affected as rapidly as those in a clayey loam. Reh (1927) claimed that injury is greater near large cities, such as Kiel and Hamburg, where leaf litter is not permitted to accumulate and where the visiting public trample the ground to a firm state. Webster (1908) stated that infestation occurs independently of whether the soil be chalky, sandy, loamy, or shaley. The writer has made no special observations on the relation of soil to infestation by *Cryptococcus fagi*.

Density of stand. The number of trees per acre and the closeness of the crown canopy seem to influence infestation only as they affect retention of moisture and protection against driving rains, hot sun, and strong winds.

That there seems to be a relation was stated by Balfour (1863), Kaltenbach (1872), and Piller and Ricker (Hartig 1880). The present writer is convinced that this is an important factor in the forest.

Position of tree in stand. For the same reasons the trees in the interior of a stand are generally more heavily attacked than those at the margins. This was recognized by Ricker (Hartig 1880), Eckstein (1920), Reichling (1920), and Bertelsmann (1913 a) who attributed it to more abundant lichens and softer bark due to greater retention of moisture.

Position of stand. The physiographic position of a stand, *per se*, seems to have little or no effect on infestation. M'Intosh (1849) found attack as uniform on high as on low ground. But where differences in the position of the stand cause changes in moisture and shelter, they influence infestation. Thus Kaltenbach (1872) found infestations to be greater on the shaded side of hillsides. Ricker (Hartig 1880) observed that when stands are sheltered infestation is heavy, independently of aspect and of whether in upland or hollow. Bertelsmann (1913 a) found infestation heaviest in stands having a southwest exposure. The British Forestry Commission (1926) agreed with earlier views that the stands sheltered from prevailing winds are most heavily attacked.

Climate. Climatic limitations are undoubtedly important in restricting the range of the woolly beech scale to parts of a large area such as Europe, where the insect has been present long enough to allow wide distribution. The possibility that changes in weather over short or long periods may affect the activities of an insect such as this one is not to be ignored. Boodle and Dallimore (1911) made the following comment:

"There can also be little doubt that climatic conditions, varying from time to time, favor its increase or decrease . . . . Thus, drought and mild winters would appear to provide the exact conditions under which it is possible for the Coccus to thrive, whilst enfeebled health of the trees (due primarily to drought and in some cases accelerated by old age) makes them peculiarly susceptible to insect attacks."

Rhumbler (1915), on the other hand, held that meteorological influences are of no importance because they act over large areas, and local differences in infestation are evidence that factors other than this are more important. The present writer agrees that local conditions exert a strong influence on infestation; but this is scarcely evidence that climatic conditions and changes in weather from year to year are without effect on the activity, fecundity, and dissemination of the insect. But this is pure conjecture. The writer has studied the disease for too short a period to allow of significant conclusions.

B. THE FUNGUS

History and Range

It cannot be stated precisely when the fungus which is causing the death of *Cryptococcus*-infested beech in the northeast first appeared, nor when it first

attracted attention, nor when it was first recognized as a species of *Nectria*. Because fatality became sufficiently conspicuous early in the last decade to attract local attention, it is probable that the fungus had been present for some years previously. So far as is known, the first report of a definite fungus associated with mortality, and its recognition as a *Nectria*, following observations in 1929 by Faull (1930) in Nova Scotia, was by the present writer (Ehrlich 1931), who collected it during 1930 in various regions throughout Nova Scotia and in Westmoreland and Albert Counties, New Brunswick. Its progress during the last three years has been followed, and by the close of 1932 the fungus had been observed in several hundred areas in Nova Scotia, including Cape Breton Island; in parts of Westmoreland and the maritime portions of Albert County, and sparsely in Queens County, New Brunswick; commonly in Washington County, and in one stand in Waldo County, Maine.* The amount and age of the fungus in these areas indicate that it is spreading rapidly in the wake of *Cryptococcus fagi*. Many of the scale-infested stands in eastern Massachusetts have been examined repeatedly and in no instance has this fungus been found. Its general range in Nova Scotia, New Brunswick, and Maine is shown in Fig. 1.

Identity

The fungus is a member of the Ascomycetous order Hypocreales, family Nectriaceae, genus *Nectria* Fries (*Creonectria* Seaver). It has been impossible as yet to determine either the precise identity of the species of *Nectria* concerned or whether it is a new species. The morphologic differences in ascospore characters and fruiting bodies among many forms in this genus are so slight that inconsistency and uncertainty have characterized the determination of species, and that cultural characters and the conidial stage have been accorded increasing importance in the recent studies of Wollenweber (1913, 1917, 1924, 1926, 1928 a, 1928 b, 1931) and Richter (1928). The fungus involved in the present investigation has been determined to be a close relative of the common, weakly parasitic, small-ascospored species, *N. coccinea* (Pers.) Fries, as delimited by Wollenweber (1928 a) and Richter (1928). Wollenweber, himself, examined a dry specimen of this fungus in 1929 and identified it as this species. As a result of extensive culturing and examination, the opinion is ventured by the present writer that this fungus differs sufficiently from *N. coccinea* to raise the question of its possible varietal status. Without further comparative studies, however, neither a clear differentiation nor a new name is proposed. In the more general characters of pathogenicity, perithecial color, perithecial size and shape, and growth in culture, it agrees well with the basic species, *N. coccinea* (Pers.) Fries, and its conidial stage, *Cylindrocarpon candidum* (Link) Wr. In addition, the ascus has the characteristic elongate flat top of this species; the ascospore length agrees satisfactorily (the mean of 590 measurements on 16 specimens being 11.9μ, in comparison with Wollenweber's mean of 11.4μ and Richter's, of 11.6μ); and the slightly curved outline of the *Cylindrocarpon* conidia and their width of

**The infected areas in Maine were discovered by Mr. H. B. Peirson, the State Entomologist.*

5.0μ–6.0μ are in agreement with similar characters of *N. coccinea*. With *N. coccinea* (Pers.) Fr. var. *longiconia* Wr., the beech *Nectria* agrees in the punctate endospore membranes of the ascospore and in the occasional presence of chlamydospores. The mean lengths of the macroconidia are exceptionally great, even greater than those reported for this variety. Some comparative measurements are given in Table XI. The color of the mycelium

TABLE XI

COMPARISONS OF MACROCONIDIAL MEASUREMENTS OF *N. coccinea* VAR. *longiconia* AND THE *Nectria* ON *Fagus* IN EASTERN AMERICA

Number of septa	*N. coccinea* var. *longiconia*		*Nectria* on *Fagus* in America
	Richter	Wollenweber	Ehrlich
3	38×5.3 (29–50×4–6)	38×4.2 (20–54×3.5–5)	—
4	55×5.8 (40–77×4.7–7)	—	62×5.0 (48–82×4.2–6.0)
5	68×5.9 (50–82×5–7)	64×5.8 (51–75×5–6)	80×5.3 (50–115×4.6–6.0)
6	81×6.5 (73–93×6–7.5)	—	91×5.7 (59–120×5.1–6.2)
7	92×6.2 (83–106×5.7–6.5)	84×5.8 (75–100×5–6.5)	100×6.0 (66–125×5.3–6.6)
8	100×6 (97–111×5.5–6.5)	—	—
9	—	101×6.0 (82–110×5–7)	—

of the beech *Nectria* in culture is distinctive, being white for the first few days, and then turning to various shades of red brown; this character distinguishes it not only from all other species grown by the present writer, but also from *N. coccinea* and its varieties as described by Wollenweber (1928); in this it resembles his *N. punicea* (Schm.) Fr. The beech *Nectria* hardly agrees with Seaver's (1910) description (ascospores 12–16μ in length) of *Creonectria coccinea* (Pers.) Seaver, or indeed with that of any other of his North American Nectriae.

Until more is learned concerning other European and American forms (a subject under investigation by the writer), it cannot be known whether this species is a native one which has been favored recently in the northeast by the increasing activity of *Cryptococcus fagi*, or an introduced species uncommon in Europe which has found scale-infested bark of *Fagus grandifolia* under climatic conditions in northeastern America a more favorable substratum than that of *F. sylvatica* in western Europe.

DESCRIPTION

The perithecia vary in shape from globose to ovoid and taper somewhat apically into an ostiolar papilla whose cells exhibit weakly radial arrangement. They are borne in clusters on discoid, subphellar, erumpent stromata. When fresh, their color is a bright, light red; with age, they darken to a drab, dark, fuscous shade. Their size ranges mostly between 200 and 300μ in width (mean 286μ, extremes 115–397μ), and between 250 and 400μ in length (mean 346μ, extremes 167–496μ).

The asci (Fig. 11 A) are eight-spored, the spores being uniseriately arranged until maturity, when the terminal two or three are crowded laterally into the

apex. The ascus is terminated by a sterile truncate apical portion which is occupied by the spores shortly before they are discharged.

The ascospores (Fig. 11 B, C) are oval to elliptical in outline, two-celled, slightly constricted at the septum; in germination they swell and increase in width before terminal or lateral germ tubes evaginate. The endospore membranes are more or less distinctly punctate or minutely echinulate. The mean length of 590 ascospores was found to be 11.9μ, with a maximal range of 7.3–16.1μ and the means of individual samples ranging between 10.5 and 12.7μ. The widths of 415 ascospores had a mean of 5.7μ with extremes of 4.1 and 7.5μ, the sample means between 4.8 and 6.2μ; these figures may be somewhat high owing to swelling attendant on incipient germination in certain samples.

Microconidia (Fig. 11 D) are formed soon after germination of the ascospores. They are borne aerially on the mycelium on the tips of short branches and are typically unicellular; occasionally they become one or more septate, especially before germination, and grade into the shorter macroconidia. Their germination is sometimes attended by fusion of the germ hyphae (Fig. 11 E).

The macroconidia (form genus *Cylindrocarpon* Wr.) are produced in nature on short conidiophores arising from a subphellar erumpent sporodochium; they are hyaline and appear white in mass. In agar cultures they arise at first on the aerial mycelium and later on small sporodochia from which they well forth as white to golden

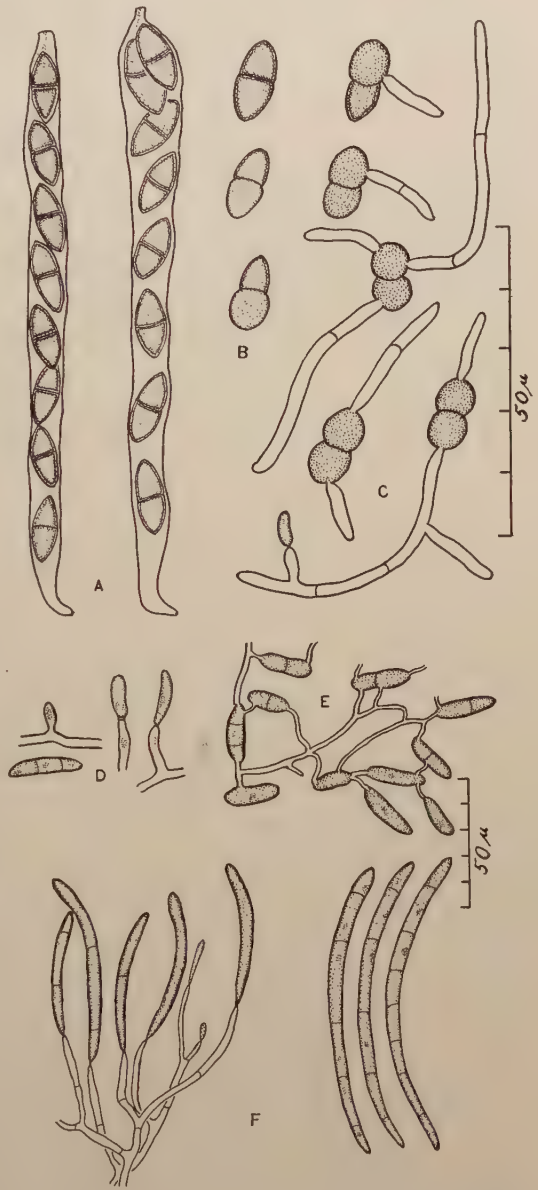

FIG. 11. *A. Asci of Nectria. B. Ascospores. C. Germinating ascospores. D. Microconidia. E. Occasional fusion of microconidial germ tubes. F. Macroconidia.*

yellow pionnotes which rise in columns to a height at times of a centimetre and dry as strands which tend to split apart. The macroconidia are elongate, slightly curved, usually three- to nine-septate (mostly five- or six-), rounded at the distal extremities, and truncate or occasionally slightly swollen at the proximal end (Fig. 11 F). Some measurements of macroconidia are summarized in Table XII. The majority range in length between 60 and 90μ; in width, between 5 and 6μ. Standard errors were computed for most of the sample means and found in all cases to be approximately 1% of the means.

TABLE XII

MEASUREMENTS OF *Cylindrocarpon* CONIDIA

Number of septa	Lengths					Widths			
	Number measured	Number of samples	Mean length, μ.	Range of sample means, μ.	Maximal range, μ.	Number measured	Number of samples	Mean length, μ.	Maximal range, μ.
4	100	2	**62**	—	48–82	20	1	**5.0**	4.2–6.0
5	549	7	**80**	67–93	50–115	40	2	**5.3**	4.6–6.0
6	343	5	**91**	84–101	59–120	20	1	**5.7**	5.1–6.2
7	139	3	**100**	90–108	66–125	20	1	**6.0**	5.3–6.6

ARTIFICIAL CULTURE

This species has been isolated repeatedly from ascospores and macroconidia produced on *Fagus* bark, and from infected bark and wood; monosporial and polysporial isolations have been made; subcultures from microconidia, macroconidia, ascospores, and mycelium produced in culture have been maintained. The media employed included autoclaved twig and branch sections of *Fagus grandifolia* and *F. sylvatica*, potato plugs, Cayley's glycerine potato plugs, potato agar, potato dextrose agar, rice agar, rice dextrose agar, cornmeal agar, oat agar, prune agar, and Czapek's agar. Although growth occurred on each of these media, the most vigorous and fecund aerial and surface mycelium developed on *Fagus* twigs and on the potato and prune agars. The simplest and most satisfactory medium was potato dextrose agar; this has been used for maintaining stock cultures. Transfers held at 33° C. made practically no growth; those at 27° C. began growing more rapidly than others kept in the laboratory, but were overtaken after a week by the latter.

In artificial culture on potato agar, a white aerial and surface mycelium develops, producing microconidia aerially in the first week. As the mycelium advances, the older portions become yellowish and then reddish brown, and the same colors infuse the agar. In about one month most cultures produce small reddish stromata at the surface of the substratum. Some of these become covered with white aerial hyphae; others develop into sporodochia on which macroconidia are produced, usually in viscous white, cream-colored, or golden streams which rise from the surface as typical pionnotes (Plate IX, Fig. A) and ultimately dry *in situ*, sometimes bent (Plate IX, Fig. B), some-

times split into longitudinal shreds. Perithecia are not produced consistently, but frequently mature at the bases of the pionnotes, in clusters on other stromata, or singly on the surface mycelium; ascospores are usually discharged in drying slant cultures or Petri plates as plugs or tortuous tendrils (Plate IX, Fig. C).

Since field studies during the winter months were not made, the possible influence of low temperatures on ascospore discharge and germination, and on macroconidial germination was examined in the laboratory. In an ascospore test, temperatures between 0° C. and 14° C. were maintained in refrigerators which fluctuated less than 1° C.; the 20° C. level was held in a water bath; and the 24° C. level was approximated in an insulated chamber in the laboratory. The procedure consisted in holding a piece of bark bearing ripe perithecia at the appropriate temperature for an hour before the start, then placing it on moist filter paper in the lower half of a Petri plate and covering with a Van Tieghem ring and cover slip; examination was made by removing the ring and focusing on the underside of the cover slip with a microscope. The data on this test are neither sufficiently numerous nor the conditions adequately controlled to warrant quantitative consideration; they show that ascospores are discharged at temperatures decreasing almost to the freezing point of water and that between 12° and 24° C. the rate of germination tends to increase with temperature.

In tests with freshly discharged ascospores in hanging drops, delayed and sluggish germination took place in a small proportion of the spores at 8° C. Between 12° and 24° C. the mean rate of growth of the germ tubes tended to vary with temperature.

Macroconidia will germinate at temperatures as low as 3° C. The results of a test with macroconidia from fresh pionnotes in culture, germinating at low temperatures in hanging drops, show that both duration of the period before germ-tube emergence and the percentage of spores germinating vary with increases in temperature, the former decreasing, the latter increasing.

Since the violence of ascospore discharge is a factor determining the importance of air currents as an agent of dissemination, several tests were made of the vertical height to which ascospores are raised when discharged from perithecia on small cubes of bark placed in Van Tieghem cell moist chambers. The distances were measured by building up the rings to graded 0.5 cm. heights and examining the cover slips for spores. In such tests the spores often reached a cover slip raised 2.5 cm. above the perithecia, but never higher ones.

Frequent observations indicated that spores at the surface of a drop germinate more rapidly than submerged individuals, a situation probably related to aeration. The relation of the distance of the spore from the atmosphere, to germination, was measured by placing a cover slip over a drop suspension of freshly discharged ascospores and making observations, at points on a straight line across the cover slip, on percentage of germination

and length of germ tubes after a given interval of time. Both measurements decrease with increased distance from the exposed edge of the cover slip.

The possible influence of hydrogen ion concentration was examined by placing a drop of uniform macroconidial suspension in the centre of each of a series of eight Petri plates ranging in pH from 2.2 to 9.6, and holding the plates at 12° C. In this test the fungus was able to develop between pH limits of 4.5 and 9.6, maximum growth taking place at 8.0.

Spore Liberation and Dissemination

Since it had been learned that ascospores are forcibly discharged from mature perithecia whenever they become moistened, it was decided to examine the occurrence of discharge in the field and its possible relation to weather conditions. The procedure consisted in placing traps over clusters of ripe perithecia on infected bark and making periodic microscopic examinations, as well as observations on general weather conditions and moistness of the bark. The trap was an ordinary 2 by 1-in. microscope slide held in place on a wood lath by a strip of aluminium tagging tape bent at both ends; the lath was secured to the trunk by a single large nail which permitted swinging into position during a test, and away from the discharge area for changing slides. With copious discharge, slides frequently became covered so densely with ascospores as to appear splashed with whitewash. The results of one such series of tests with 12 traps during the summer of 1931 in Kings County, Nova Scotia, are presented in Table XIII. The last days of July were dry, with the exception of showers on July 26, which failed to wet the bark. In order to be certain that the apparently mature perithecia were actually capable of spore discharge, four of the test areas were slightly moistened artificially, and two of them gave appreciable ejections. The first rain (on August 4) of sufficient magnitude to wet the trunks of the beeches under examination resulted in copious discharges which dwindled progressively on the following two days, although they continued lightly on certain areas even after the surface of the bark appeared dry. A lighter rain on August 10 resulted in renewal of discharge on all of the test areas which became wet, and continued on the following day in spite of surface drying.

Weather-vane spore traps were set in conjunction with the foregoing tests to yield information on possible air dissemination of the spores. These traps were modified from similar ones used by the Canadian Department of Agriculture; they consisted of a galvanized iron box open at both ends, with a sliding bottom, and containing centrally on the two sides two slotted holders for a microscope slide; one end was equipped with a large vertical sheet of metal for a weather vane, and the other accurately counterbalanced with lead. The trap was suspended by a hook soldered into the top, and a chain made by twisting baling wire into large rings. It was suspended from a branch and guyed to prevent swaying. This method of suspension was found to be far more sensitive in orientational response to the lightest air currents than the usual more complicated, heavy, and expensive upright ball-bearing equipment. The microscope slide in such a trap always faces

TABLE XIII

ASCOSPORE DISCHARGE RECORDS; KINGS CO., N.S.; JULY-AUGUST, 1931

Month	July					August						
Date	25	26	27	28	31	4	4	5	5	6	10	11
Hour	10 a.m.	11 a.m.	6 p.m.	3 p.m.	11 a.m.	11 a.m.	5 p.m.	11 a.m.	7 p.m.	7 a.m.	11 a.m.	11 a.m.
Weather during preceding interim	Sunny, windy, muggy	Showers, muggy	Sunny, windy, hot	Sunny, windy, hot *(a)*	Cloudy, windy, cool	Sunny, cool; 3-4p.m., rainy, muggy	Sunny, breeze, warm	Sunny, breeze, warm	Sunny, breeze, hot	Sunny, breeze, cool	Sunny, rain, cool	Sunny, cloudy
Condition of bark	Dry	Dry	Dry	*(a)*	Dry	All wet	Wet under traps	Moist under some	Dry	Dry	Moist in spots	Dry
Bark traps												
126E–A	0	0	0	*a* 0	0	3	2	0	0	0	*m* 0	0
126E–B	—	0	0	0	0	3	2	*m* 2	1	0	0	0
127E–A	0	0	0	*a* 3	0	3	2	*m* 2	2	1	0	0
127E–B	—	0	0	0	0	3	2	0	0	0	*m* 1	0
128E	0	0	0	0	0	3	3	*m* 3	2	0	*m* 3	3
129E	0	0	0	0	0	2	2	2	2	0	*m* 2	2
130E–A	0	0	0	*a* 0	0	2	2	0	0	0	0	0
130E–B	—	0	0	0	0	2	2	*m* 1	0	0	*m* 1	2
131E–A	0	0	0	*a* 2	0	3	2	2	1	0	0	0
131E–B	—	0	0	0	0	1	1	1	0	0	*m* 1	2
132E	0	0	0	0	0	3	1	*m* 0	0	0	*m* 2	2
133E	0	0	0	0	0	3	2	0	0	0	*m* 3	3

Key to abbreviations: a, artificially moistened; m, moist; —, no observation; 0, *no discharge;* 1, *light discharge;* 2, *medium discharge;* 3, *copious discharge.*

the wind and is protected against being washed by rain and against falling debris. Such traps were hung at various elevations and positions in the stands being tested for ascospore discharge in the hope that they might yield collatable data on air dissemination. No ascospores were caught in the Kings County tests. Subsequent success elsewhere justifies the opinion that the relatively few beeches with mature perithecia in the long-infected and largely decimated stands in Kings County supplied insufficient spores for measurement in so minute a sampling of the atmosphere.

These tests were repeated during August, 1931, in a more recently infected beech stand in Inverness County, Nova Scotia. The results are presented in Table XIV. Here, as in the foregoing tests, rains of sufficient magnitude to wet the bark of the trunks resulted in spore discharge, which continued in some cases for three or four days after the bark surface had become dry. Macroconidia from fresh pustules were present on these trees and were caught in smaller numbers and for shorter periods following the rains. It is not known whether they are abstricted explosively or merely dislodged and caught by air currents; the simple manner of formation on the tips of conidiophores suggests the latter explanation.

Negligibly few spores were caught in the weather-vane traps following the first rain. The catch during and after the second rain on August 26 included ascospores and macroconidia in sufficient numbers to demonstrate conclusively that both spore forms are carried by air currents. It is very probable that when rainy weather lasts for two or more days, enabling discharge, dissemination, and germination in suitable inoculation courts, the dissemination of spores by air currents provides the most important method of spreading the fungus from tree to tree and possibly from stand to stand.

It is not unlikely that animals such as insects, arachnids, birds, and rodents occasionally act as unwitting carriers of the fungus. There is no direct evidence for or against this possibility, but the varied and active arthropod fauna on forest beech strongly suggests its correctness. Tests to determine whether crawlers of *Cryptococcus fagi* carry spores were attempted but yielded no conclusive data. That the crawlers are not specific vectors appears probable to the present writer. Only on heavily infested trees which have become lightly infected by the *Nectria* and support fresh sporodochia and perithecia in limited areas are there still healthy portions capable of nourishing *Cryptococcus* colonies; larvae hatched on such trees undoubtedly carry spores on their bodies and may thus transport inoculum to fresh bark on the same or other trees. That this is an important means of local dissemination appears unlikely.

Long range distribution of the fungus may possibly be effected by wind, birds, or man. Nothing is known of it.

TABLE XIV

ASCOSPORE AND MACROCONIDIUM DISCHARGE AND CATCH RECORDS; INVERNESS CO., N.S.; AUGUST, 1931

Month	August								
Date	20–21	21	21	22	22	24	25	26	27
Hour	5 p.m.-9 a.m.	2 p.m.	5 p.m.	10 a.m.	5 p.m.	10 a.m.	9 a.m.	10 a.m.	2 p.m.
Weather during preceding interim	Rain	Showers, sunny, windy	Sunny, windy	Sunny, breeze	Sunny, breeze	Sunny, breeze	Sunny, breeze, cloudy	Rain	Sunny, breeze
Condition of bark	All wet	Moist in spots	Moist in spots	All dry	All dry	All dry	All dry	All wet	Drying
Bark traps									
134E–A	3	*m* 3	*m* 1	0	0	0	0	3	2
134E–B	3	3	1	0	0	0	0	3	2
134E–C	2 *C**	*m* 3	*m* 2	2	1	1	0	3 *C*	2
135E	2 *C*	1	0	0	0	0	0	2 *C*	1
136E–A	3 *C*	*m* 3 *C*	*m* 3	2	2	2	0	3 *C*	3
136E–B	3 *C*	3 *C*	1	0	0	0	0	3 *C*	3
136E–C	3 *C*	3 *C*	0	0	0	0	0	3 *C*	2
136E–D	3 *C*	3 *C*	*m* 2	1	0	0	0	3 *C*	2
136E–E	2 *C*	*m* 2 *C*	*m* 1 *C*	1	1	0	0	2 *C*	2
137E–A	3 *C*	*m* 0 *C*	0	2	1	1	1	3 *C*	3
137E–B	3 *C*	*m* 2	*m* 2	2	0	0	0	3 *C*	2
138E	3 *C*	1 *C*	0	0	0	0	0	2 *C*	2
Aerial weather-vane traps†									
1	0	—	0	—	—	—	—	11	—
2	0	—	2	—	—	—	—	5	1
3	0	—	1	—	—	—	—	34, 11*C*	3
4	0	—	0	—	—	—	—	77, 4*C*	0
5	0 *C*	—	0	—	—	—	—	54	3
6	0 *C*	—	1	—	—	—	—	8, 5*C*	1

**C : macroconidia (Cylindrocarpon).* †*Recording actual numbers of spores caught.*

C. PATHOGENICITY

Outline of the Proof of Pathogenicity

The proof of the role played by each of the two pathogens in the beech bark disease rests on extensive field observations and on experiments in the field and greenhouse. The evidence supports the etiologic theory that the woolly beech scale, *Cryptococcus fagi* (Baer.), alone is not fatally pathogenic but is the initial agent, predisposing the tree to infection by the *Nectria*, which—once established—grows parasitically and causes death by destruction of the protective, storage, and vascular systems of the trunk and larger branches. The nature of the evidence adduced in support of this theory is summarized in the following outline.

A. *Cryptococcus fagi* is the initial essential agent under field conditions, but alone does not cause death.

1. *Nectria* infection occurs in nature only on *Fagus* bark contemporarily or previously infected by *Cryptococcus;* mortality typically follows *Nectria* infection.
2. Where *Cryptococcus* is not followed by *Nectria*, death rarely occurs.
3. Field and greenhouse inoculations of clean intact bark failed to produce infection.
4. Preliminary field inoculations of *Cryptococcus*-infested bark with *Nectria* spores resulted in infection.
5. Areas of bark on trunks of uninfested trees, protected against subsequent infestation, remained uninfected, while exposed areas on the same trees became infected.
6. Areas of bark on trunks of artificially disinfested trees, protected against subsequent infestation, became infected, but less abundantly than exposed areas on the same trees.

B. A species of *Nectria (coccinea* group) infects bark infested by *Cryptococcus fagi*, is able to grow parasitically, and is immediately responsible for tissue necrosis and mortality.

1. Signs and symptoms of infection by this species of *Nectria* develop in nature on a preponderant majority of the *Cryptococcus*-infested trees in the regions known to harbor this fungus.
2. The fungus has been repeatedly isolated from naturally inoculated bark and wood which had or still harbored the insect, and has been grown in pure culture to fruiting stages.
3. Artificial field and greenhouse inoculations on intact bark resulted in no infection; but similar inoculations on mechanically wounded and on *Cryptococcus*-infested bark produced infection, and in some cases fruiting bodies. The fungus was reisolated from infected tissues and fruiting bodies, and grown in pure culture.

Role of Cryptococcus fagi

Field observations

Cryptococcus alone. Many of the early accounts of *Cryptococcus fagi* in Europe report trees infested for periods of one and two decades without suffering apparent injury. In more recent times the conclusion was reached in England by Boodle and Dallimore (1911) and in Germany by Bertelsmann (1913 a), Rhumbler (1914, 1915, 1922, 1931), and others that the insect alone produces little or no damage but that fungi, which gain entrance to the living tissues as a result of insect attack, are the immediate pathogens. No experimental evidence in support of this conclusion has been reported. The same opinion is fully borne out by the situation observed in America by the present writer. Here a particular species of *Nectria* has become so abundant and widespread in Nova Scotia and New Brunswick that it fatally infects trees attacked by *Cryptococcus* with such speed and severity as to have resulted in a veritable epiphytotic. In eastern Massachusetts, on the contrary, the fungus has not been discovered and many trees which are known to have been infested by the insect for at least four years show no serious effects.

Nectria following Cryptococcus. Many fungi have been reported in Europe as causing injury to *Cryptococcus*-infested beech; but among them, beginning with Hartig (1880), species of *Nectria* (usually referred to *N. ditissima* Tul.) have been accorded the greatest importance. It is unlikely that the species which has become widespread in the Maritime Provinces is the same as those found in Europe (as explained in Section VII B, above). This species has been found by the present writer only on bark of *Fagus grandifolia* contemporarily or previously infested by *Cryptococcus fagi*, and only in Nova Scotia, New Brunswick, and Maine. The fungus is associated in the great preponderance of cases with death of the infested trees. This fact is not proof of the contention that *Cryptococcus* is an essential agent in the Maritime outbreaks of the beech disease, but constitutes supporting evidence of experimental proofs submitted below.

Inoculations on Clean Intact Bark

The first question to be decided experimentally was whether or not this *Nectria* is capable of penetrating the corky layer of the bark and producing infection. The possibility was tested with forest beeches at Fredericton, New Brunswick, beyond the range of *Cryptococcus fagi*, and on a great many occasions with potted sapling beeches (both *Fagus grandifolia* and *F. sylvatica*) in the greenhouses at Harvard University.

Field inoculations were made with ascospore suspensions, with pieces of infected bark secured so that the ostioles of mature perithecia were in contact with the inoculation courts, and with macroconidial masses from natural pustules and from pionnotes in culture. The inoculation courts were clean areas of bark which had never been attacked by *Cryptococcus fagi;* they were lichen-free, lichen-covered, or lichen-freed. The inoculum was applied

to marked courts on the previously moistened bark, and covered with layers of wet absorbent cotton and wrapped in factory cotton or oilcloth. They were examined after two months or in the following year. In no case had infection resulted.

Greenhouse inoculations were made with ascospores and macroconidia on lichen-free bark of potted saplings. In the early tests the courts were wrapped with wet absorbent cotton and raffia; in the later ones, the courts were inclosed in celluloid cylinders sealed at top and bottom with wet cotton or sphagnum (Plate IX, Figs. F, G) or the saplings placed in a tent within which the atmosphere was kept saturated by a continuous flow of water over the canvas (Plate IX, Fig. D). Not a single infection developed.

Inoculations on Cryptococcus-infested Bark

If *Cryptococcus*-infested bark known to be uninfected by the *Nectria* could be successfully inoculated, this would be proof that the insect enables the fungus to infect bark otherwise resistant. Such inoculations should be made on trees in a region infested by the insect but free of the fungus. Eastern Massachusetts is an ideal region for this purpose; but the writer refrained from carrying out such an experiment out of doors because of the possibility that the dangerous species of *Nectria* might inadvertently be liberated and become established locally. Field inoculations were made in the Maritime Provinces and greenhouse inoculations at the Arnold Arboretum.

Field inoculations were made in Digby and Inverness Counties, Nova Scotia, and in Albert County, New Brunswick, on recently infested trees which at the time of inoculation showed neither symptoms nor signs of *Nectria* infection. The insects were not disturbed in certain tests; in others they were removed by scrubbing with a contact insecticide followed by an aqueous wash. Inoculation courts were protected against reinfestation and natural fungal inoculation by wrapping in tarred factory cotton (Plate IX, Fig. H) or tar-sealed oilcloth. The great majority of these artificial inoculations were followed by definite lesions and fruiting bodies of the *Nectria*. But the conclusiveness of these results is not entirely satisfactory because in many cases the bandaged control areas, consisting of insect-infested bark not artificially inoculated, also became infected, indicating that natural inoculation had preceded the artificial tests. Unquestionably this experiment should be repeated in an area where there is as yet no possibility of natural *Nectria* infection. Nevertheless, successful inoculations with uninfected controls, secured in certain of the tests, are reliable evidence that the fungus is able to infect insect-infested areas of bark, since even a single clear cut positive result is significant in itself, and the contamination of other tests is not evidence against the positive result.

Greenhouse inoculations. The difficulty of finding a satisfactory location for field inoculations in the Maritime Provinces, and reluctance to perform them in eastern Massachusetts increased the desirability of greenhouse experiments where the danger of liberating the fungus could be held at a

minimum. In 1932, pieces of heavily infested bark harboring hatching eggs were removed and tied to potted saplings in the greenhouse. An abundant transfer of crawlers took place and many settled on the saplings and secreted wool, the number being greatest on saplings kept in the moist chamber tent. As yet the insect has not become sufficiently established to warrant performing inoculations.

Protection Experiments on Uninfested Bark

If areas of bark on as yet uninfested or newly and lightly infested trees in regions recently attacked by *Cryptococcus fagi* and the *Nectria* could be protected from subsequent infestation, but not from *Nectria* inoculation, the absence of *Nectria* infection on these areas, at the same time that adjacent unprotected areas on the same trees became infested and infected, would constitute additional evidence in support of the view that the insect is an essential initial factor in *Nectria* infection. This possibility was tested by selecting two uninfested trees and two very lightly infested ones on which the insects were removed from the area to be protected; an area on the trunk three feet vertically at convenient height was wrapped in phosphor-bronze wire cloth (120 mesh per inch) in such a way that it came into contact with the bark only at the top and bottom ends, which were coated with Tanglefoot (Plate IX, Fig. I). This material was renewed occasionally. A few nymphs were able to crawl through infrequent larger apertures, but for the most part protection was excellent. Examination after 15 months consisted in counting the numbers of lesions visible on the surface of an area two feet high under the screen, and an area one foot high immediately above the screen, shaving the bark below the phelloderm and counting (Plate IX, Fig. J), and finally removing the bark and counting the lesions visible on the surface of the wood. The pertinent data on this experiment are presented in Table XV. It will be seen from the table that although a few small

TABLE XV

EFFECT ON *Nectria* INFECTION OF PROTECTING BARK AGAINST *Cryptococcus* INFESTATION

Tree no.	Protected May 12, 1931.	Examined August 25, 1932				
		Protected area		Adjacent unprotected area*		
					Nectria infection	
	Cryptococcus infestation	*Cryptococcus* infestation	*Nectria* infection	*Cryptococcus* infestation	Lesions in bark	Lesions to wood
213 E	None	Very light	None	Medium	5	3
214 E	None	Very light	None	Medium	0	0
237 E	Very light (removed)	Very light	None	Medium	>200	90
238 E	Very light (removed)	Very light	None	Medium	>200	56

**Since the area examined was only half as great as that under the screen, the number of lesions has been doubled.*

colonies of the insect developed in the protected areas, not a single *Nectria* infection resulted, while in the adjacent unprotected areas on the same trees the insect increased in numbers and fungal lesions appeared in varying quantities. This is taken to be evidence supporting the view that the continued feeding of *Cryptococcus fagi* enables otherwise impossible *Nectria* infection.

Protection Experiments on Disinfested Bark

A similar experiment was made on trees infested with *Cryptococcus* but exhibiting neither symptoms nor signs of *Nectria* infection. Five trees were selected, ranging in amount of infestation from light to heavy. The insect was removed from an area of trunk surface three feet vertically, and the area protected with a phosphor-bronze screen. When the trees were examined after 15 months (Table XVI), reinfestation of the supposedly protected areas was observed to have taken place to a small extent; but, in spite of this, the results, although variable quantitatively, showed a consistently greater infection of the adjacent unprotected areas than of those protected. This experiment, also, is interpreted as evidence supporting the contention that under forest conditions the ability of the *Nectria* to infect is dependent on feeding by *Cryptococcus fagi;* it shows, further, that previous feeding by the

TABLE XVI

EFFECT ON *Nectria* INFECTION OF PROTECTING PREVIOUSLY INFESTED BARK AGAINST *Cryptococcus* INFESTATION

Tree no.	Disinfested and protected May 13, 1931. *Cryptococcus* infestation	Examined August 22, 23, 1932					
		Protected area			Adjacent unprotected area*		
		Cryptococcus infestation	*Nectria* infection		*Cryptococcus* infestation	*Nectria* infection	
			Lesions in bark	Lesions to wood		Lesions in bark	Lesions to wood
261 E	Light	Light	78	6	Medium	>200	20
262 E	Light	Light	6	6	Medium	>200	104
304 E	Medium	Light	24	0	Medium	140	0
284 E	Heavy	Light	9	0	Heavy	>200	26
285 E	Heavy	Medium	88**	21	Extra heavy†	much >200††	>200

**Since the unprotected area examined was only half as great as that under the screen, the number of lesions has been doubled.*

***Twenty-four surface lesions with Cylindrocarpon sporodochia.*

†Many colonies already dead because of drying of substratum.

††So largely coalesced that 90% of area necrotic; many surface lesions with sporodochia and fresh perithecia.

insect—when of sufficient intensity and duration—makes possible subsequent fungal infection.

ROLE OF NECTRIA

Field Observations

The symptoms of this disease develop only in regions known to harbor the particular species of *Nectria (coccinea* group) under discussion, and in

these regions only on trees infected by this fungus. Development of this fungus, observed in nature exclusively on trees attacked by *Cryptococcus fagi*, precedes the appearance of systemic symptoms of mortality (in the crown), continues with the progress of such symptoms, and ceases soon after the production of holonecrosis in the immediate substratum, and death of the tree. Such behavior is characteristic, not of a saprophyte, but rather of a parasite lacking only the ability to effect penetration of normal intact bark. These observations alone are not proof of the pathogenicity of the fungus, but strongly support the experimental evidence.

Isolation from Naturally Infected Tissues

Additional evidence, in agreement with experimental results, is afforded by the constant association of the fungus with necrotic lesions on the bark of *Cryptococcus*-infested beech. Conidial and ascigerous fructifications of the *Nectria* alone develop on the great majority of such lesions; when the fungus is artificially cultivated from the spores of such fructifications, spores are produced in culture. Aseptic tissue plantings from such lesions, and in the Maritime Provinces from the freshly necrotic margins of slime-flux lesions, regularly give rise to typical fruiting cultures of the fungus, similar in every respect to those secured from spore isolations.

Inoculations and Reisolation

Inoculations on intact bark. It has been pointed out above that inoculations with macroconidia and ascospores of the *Nectria* on clean intact *Fagus* bark fail consistently to result in infection. Although this is negative evidence, the fact that other inoculations on ruptured bark were successful lends reliability to the negative results. They are interpreted to demonstrate that the fungus is incapable of infecting sound bark of beech.

Inoculations on mechanically wounded bark. If the theory that the feeding of *Cryptococcus fagi* exerts no specific chemical or biological influence on the resistance of the bark to *Nectria* infection, but merely breaks down the mechanical barrier of the phellem, be true, artificial inoculation of mechanically injured bark should result in infection. Such infection would also be evidence of the ability of the fungus to grow parasitically, once the phellar barrier is broken. Accordingly, healthy bark was subjected to injury ranging from superficial needle punctures of the phellem to scalpel slits penetrating to the cambium. The methods of inoculation were similar to those described above. The inoculations, performed in affected parts of the Maritime Provinces, were protected against subsequent natural inoculation by wrapping with tarred factory cotton or tar-sealed oilcloth. Others were made at Fredericton, New Brunswick, beyond the range of the pathogens. Still others were set up in the greenhouses at Harvard University. These inoculations were followed almost invariably by infection; further, the fungus spread for distances attaining several centimetres periclinally, and often into the wood. The appearance of one trunk, wounded before inoculation by scraping of the periderm, showed, when examined after nine months, that infections had pene-

trated in several patches to the surface of the wood (Plate IX, Fig. E, photographed after bark had been peeled from the wood). Greenhouse inoculations were frequently followed by the production of macroconidial sporodochia and mature perithecia on the infected tissues; in certain cases the fungus maintained itself and advanced slowly for two or three years, and could be induced to fruit again by inclosing the infected area in a celluloid cylinder moist chamber or placing the saplings into the moist chamber tent. These experiments, together with the results of inoculating *Cryptococcus*-infested bark, yield evidence that the role of the insect is mechanical rupturing of the periderm, attendant on death and shrinkage of the probed tissues. They demonstrate, further, that the fungus is able, under experimental conditions, to infect bark whose periderm has been ruptured, to spread parasitically, and to fruit.

Inoculations on Cryptococcus-infested bark. The results of preliminary inoculations on *Cryptococcus*-infested bark, described above, contribute to the evidence that the *Nectria*, although incapable of penetrating intact bark, is able to infect tissues on which the insect has been feeding.

Reisolation of the fungus following artificial inoculation. Following a number of the inoculation experiments, the fungus was reisolated, both from infected tissues and from macroconidia and ascospores produced on the infected tissues. The fungus was grown in pure culture and its mycelium and spores found to be entirely similar to those in original cultures. In a few cases, inoculations with spores from the same reisolation cultures were made; infection resulted and the fungus was reisolated a second time. These results are regarded as final proof that the species of *Nectria* under consideration is able to infect *Fagus* bark whose periderm has been ruptured either artificially or by tearing of the periderm attendant on death and shrinkage of *Cryptococcus*-probed tissues.

Summary

It has been demonstrated that the beech bark disease in northeastern America results from the sequent activity of two pathogens, the woolly beech scale, *Cryptococcus fagi* (Baer.), and a species of *Nectria (coccinea* group). The evidence for the role of each of these organisms, outlined at the beginning of this section, consists of (1) constant association of the organisms with the disease, (2) the absence of the disease when only one is present, (3) the consistent isolation of the fungus from infected tissues, and (4) the inability of the fungus to infect tissues not infested by the insect, and its ability to infect those infested. The role of the insect has been shown to be the rupturing of the periderm attendant on death and shrinkage of the living cells of the bark on which the insect feeds. This enables initial infection by the fungus. The role of the fungus is the causing, by parasitic growth, of death and destruction of the storage and vascular systems of the trunk and branches.

D. COURSE OF THE DISEASE

Protection Experiment

The question of determining how long a period of time elapses between first attack by the insect and initial fungal infection is partially elucidated by a field experiment. Eight small experimental plots were selected, ranging in amount of *Cryptococcus* infection from none to heavy, and in duration to at least three years, and showing no indications of *Nectria* infection. Areas extending three feet vertically on the beech in these plots were disinfested by scrubbing (except the originally uninfested trees) and were protected against subsequent infestation and infection by wrapping in tarred factory cotton or oilcloth. These areas and adjacent unprotected areas on the same trees were examined after 15 or 23 months by searching the bark surface for *Cryptococcus*, and for signs and symptoms of infection, then shaving the bark below the periderm and counting lesions, and finally removing the bark and counting lesions on the wood. The trees in these plots have been arranged in five classes based on initial *Cryptococcus* infestation, and the data secured at the conclusion of the experiment summarized in Table XVII. Examining the *Cryptococcus* columns, it will be seen that protection was imperfect with three trees; in all others the protected areas remained free of the insect.

TABLE XVII

Development of *Cryptococcus* and *Nectria* on protected and unprotected areas of trees with varying initial *Cryptococcus* infestation

Initial *Cryptococcus* infestation*	No. of trees	**	At conclusion of experiment						
			Per cent of trees with *Cryptococcus*					Number of *Nectria* lesions per area per tree	
			0	1	2	3	4	In bark	To wood
0	41	P†	100	0	0	0	0	**2**	**1**
		U	32	12	44	7	5	17	1
1	27	P	96	0	4	0	0	**13**	**4**
		U	11	0	30	59	0	58	19
2	22	P	91	0	9	0	0	**29**	**12**
		U	9	0	5	77	9	91	42
3	9	P	100	0	0	0	0	**40**	**11**
		U	0	0	0	67	33	121	25
4	15	P	100	0	0	0	0	**68**	**22**
		U	0	0	0	47	53	198	102

	0	*1*	*2*	*3*	*4*
**Amount of infestation*	*None*	*Very light*	*Light*	*Medium*	*Heavy*
Duration of infestation	—	*Few months*	*Approx. 1 year*	*Approx. 2 years*	*> 2 years*

***P = protected; U = unprotected.*

†*No signs or symptoms of Nectria infection when protected.*

The infestation on adjacent unprotected areas increased progressively with the amount and duration of initial infestation, except on the most heavily attacked trees; the infestation on certain of the trees in each class, except the uninfested, decreased, however, a situation related to death of infested areas of bark following their infection by the *Nectria*. Turning to the infection figures, it is evident that the number of *Nectria* lesions on protected bark also increased progressively with the amount and duration of initial *Cryptococcus* infestation, being a probably negligible 2 per area per tree on areas uninfested at the start of the experiment, 13 on areas very lightly infested for only a few months, 29 on areas lightly infested for approximately one year, 40 on areas generally infested for approximately two years, and 68 on areas heavily infested for over two years (Fig. 12). The number of these lesions penetrating to the wood is less on most trees. These figures permit no precise determination of the period elapsing under forest conditions between first insect attack and fungal infection. It will be observed, however, that not only are the numbers of lesions small on protected areas infested for less than one year at the outset, but also ratios of lesions on unprotected to protected areas are larger for the areas initially infested for less than a year ($8\frac{1}{2}$ to 1, and $4\frac{1}{3}$ to 1) than for the areas initially infested for a year or longer (approximately 3 to 1). Both of these relations suggest that the fungus infects extensively only where the insect has been present for a year or longer. This interpretation is also borne out by the data in Tables XV and XVI, which show that, with artificially disinfested bark protected against insect attack but not against fungal invasion, subsequent infection took place only when the infestation had continued for approximately one year or longer.

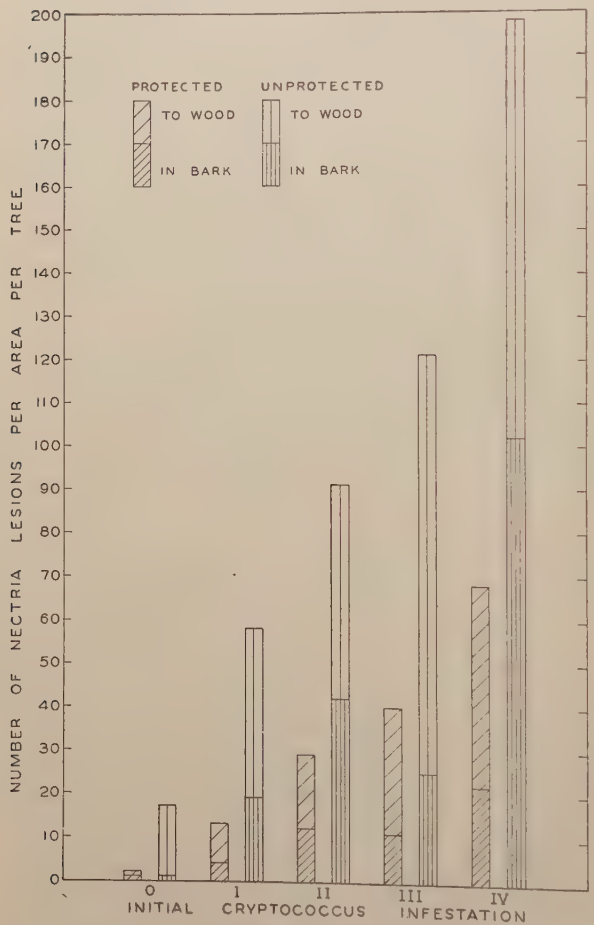

FIG. 12. *Development of Nectria on protected and unprotected areas of trees with varying initial Cryptococcus infestation.*

Permanent Sample Plots

In order to make careful and consistent observations on the development of the pathogens and the course and duration of the disease on trees of different ages in various types of stands, nine permanent sample plots were laid out, in which 1425 beech were tagged and described. Observations were made in most of the plots in each of three consecutive years and the data on each tree recorded on a specially designed, mimeographed form sheet. The plot data recorded include size, type, site quality, density, slope, aspect, drainage, soil, humus, slash, ground cover, underbrush, reproduction, and miscellaneous observations on the stand, its pathological condition, and the presence of *Cryptococcus*, *Nectria*, and other insects and fungi. The data recorded for each tagged tree include crown class, diameter (d.b.h.), various notes on foliage, branches, trunk injury, bark, mosses, lichens, *Cryptococcus fagi*, the predacious Coccinelid: *Chilocorus bivulnerus* Muls., beetle borings, other insects, slime-flux lesions, signs and symptoms of *Nectria* infection, and other fungi.

In order to show something of the information available from this mass of data, a few pertinent facts are presented on Plots 1 and 7. Certain general data appear in Table XVIII. The plots, situated in widely separated parts of Nova Scotia, are of uniform area and site quality. Plot 1 is on a steep slope, and Plot 7 is almost level. Plot 1 is composed of almost pure beech, and Plot 7 is in a typical mixed tolerant-hardwoods type. The crown densities of the two plots are similar. Plot 1 contains a much larger proportion than Plot 7 of suppressed trees. When the sample plots were laid out and first examined in 1930, Plot 1 was selected as representative of an early stage of the disease; although every tree supported the woolly beech scale, only 8.5% showed indications of *Nectria* infection and none had died. Plot 7 represented an advanced stage of the disease; many trees were already dead for more than a year and are not included in the present account; all beech were or had been infested by *Cryptococcus*, 69% were already infected by *Nectria*, and 4.8% had died of the disease in the preceding year. In 1931 (Table XIX), the amount of living insects decreased with death of certain of the affected trees; the percentage of infected trees increased sixfold in Plot 1, and by 10% in Plot 7; 2% of the trees died of the disease in Plot 1, and 11% more in Plot 7. By 1932, the percentage of infected trees had reached 76 in Plot 1 and 92 in Plot 7; mortality due to the disease claimed 3.4% in Plot 1 and 59% in Plot 7.

TABLE XVIII

GENERAL DATA ON PERMANENT SAMPLE PLOTS 1 AND 7

	Plot 1	Plot 7
Location	Inverness County, N.S.	Annapolis County, N.S.
Size	0.5 acre	0.5 acre
Site quality	I	I
Slope	100%	3%
Type	Pure beech	Beech, birch, maple
Crown density	.7	.7
Number of beech	294	147
Number (exclusive of suppressed) of beech	59	82

These data from typical beech stands show several facts regarding the beech bark disease. Those from Plot 1 indicate that, once the trees become generally infested by *Cryptococcus fagi*, *Nectria* infection develops sufficiently to produce external signs and symptoms on the majority within three years and kills some of them in one or two years. The Plot 7 data show that in the later stages of infection the majority of susceptible trees have already been infected, but that, in spite of the slower increases, almost an entire stand becomes infected. In the later stages, the amount of infection on *Nectria*-attacked trees builds up rapidly and leads to large increments in mortality.

TABLE XIX

PERCENTAGE OF BEECH INFESTED, INFECTED, AND KILLED IN PLOTS 1 AND 7

	Plot 1			Plot 7		
	1930	1931	1932	1930	1931	1932
Cryptococcus fagi (living or remains)	100	100	100	100	97	98
Cryptococcus fagi (remains only)	0.0	5.8	7.5	5.4	28	50
Nectria (symptoms or signs)	8.5	5.3	76	69	88	92
Killed by *Nectria*	0.0	2.0	3.4	4.8	16	59
Killed by all causes	0.0	5.8	7.5	5.4	22	64

When the dead beech are grouped according to size and the percentages of trees in each diameter and crown class dead computed (Table XX), the fact emerges that the percentage of beech dying as a result of the disease increases

TABLE XX

PERCENTAGE OF BEECH KILLED BY *Nectria* COMPARED WITH DIAMETER AND CROWN CLASS (PLOTS 1 AND 7, 1932)

Plot		Diameter classes				
		Sapling	1–2 in.	3–6 in.	7–10 in.	11–16 in.
1	Number of beech	102	96	51	28	17
	Per cent dead	1.0	11	39	43	35
7	Number of beech	—	39	66	31	11
	Per cent dead	—	31	51	94	100

Plot		Crown classes			
		Suppressed	Intermediate	Co-dominant	Dominant
1	Number of beech	235	17	18	24
	Per cent dead	11	41	50	38
7	Number of beech	67	28	23	29
	Per cent dead	43	75	83	93

with size of tree. By both measures of size, the largest class in Plot 1 is an exception to this trend, its percentage of beech dead being less than that of the next smaller class. The explanation of this situation may lie in the fact that the larger older trees are less severely infested and infected than somewhat smaller ones, probably because of their rougher, more corky bark. The figures for Plot 7, which has been attacked for a longer period than Plot 1, bear out this explanation both in their consistent upward trend and in their levelling off with higher size classes. These figures are based on relatively few trees, but the analysis of line-plot data (Section VIII, below) on several thousand individuals reveals the same trend.

VIII. Factors Influencing Development of Infection and Mortality

Two schools of thought exist with regard to the evaluation of the agencies which combine to induce the pathic changes which constitute a disease. One school places primary emphasis on the immediate causes of a disease, whether they be biotic or abiotic. The other school admits that the primary causal agent is a factor *sine quo non*, but contends that the complexes of other abiotic and biotic factors which influence the virulence of a disease are the more important, both scientifically and economically, since it is they which often determine the actual course and consequences of a disease. It is a fact that diseases vary in the extent to which immediate and secondary factors influence their course: in some, as with the chestnut bark disease, the mere presence of the causal fungus *(Endothia parasitica)* is sufficient to cause infection and ultimate death, regardless of such variables as age of tree, local environment, and weather; in others, the pathogen is more or less continually present and the disease becomes virulent only under particular conditions of weather (late blight of potato) and age of tree (white trunk rot of poplar). The influence of such factors can be exerted on pathogen (as with late blight), on suscept (as with white rot), or on both.

With the disease discussed here, as with others, the existence of such influences is of technical interest and possibly of practical importance in governing control measures. The influence of such factors on the habits and development of insect and fungus has been discussed in Section VII. Certain of the factors which affect the course of infection and mortality are dealt with in the following pages.

PRELIMINARY OBSERVATIONS

Preliminary observations in the course of two summers' field work led the writer to the conviction that three factors especially influence the development of the fungus and the disease; these are (1) density of stand, (2) the amount of mosses and foliose lichens on the trunk, and (3) size of tree.

It appeared that in stands with a dense crown canopy, where sunlight and warmth penetrate less readily, where drying winds are less effective, and where moisture following rains remains longer, the fungal lesions and fructifications develop more rapidly and abundantly, inoculum is more plentiful,

and conditions favoring inoculation and incubation exist. This influence of moisture was strikingly apparent in stands with minor crown openings, where, following a rain, one side of the trunk, remaining wet longer, was frequently observed to bear a continuous series of coalesced lesions and fungal fruiting bodies, while the exposed and rapidly drying side of the same trunk bore but a few delimited circular lesions with a meagre development of fruiting bodies.

Mosses and foliose lichens (see Section VII B, above) were constantly observed to favor the development of the fungus. This was assumed to operate in two ways. The first is by providing an ideal shelter for the wandering nymphs of *Cryptococcus* and the development of feeding colonies of the insect, which soon affords excellent inoculation courts for *Nectria*. The second way is by favoring directly the incubation of inoculum and infection of the suscept through providing anchorage against streams of water which run down the bark during rains, and through maintaining moist conditions long after wind and sun have dried the exposed surfaces of the trunk. The soundness of these views was borne out by examination of countless lichens and mosses. On trees with only minute and occasional insect colonies, larger and older colonies could always be found under mosses and lichens, especially the latter. On a day following heavy rains, when the exposed bark had already dried, moisture could always be found under the thalli. Shaving the bark of recently infested and newly infected trunks beneath 221 lichen thalli disclosed healthy areas under 45.7% of the thalli and necrotic areas under 54.3%; shaving under 230 mosses disclosed healthy areas beneath 31.7% and necrotic areas under 68.3%. On these same trunks the number of necrotic areas per unit of bark surface was far less for exposed bark than for bark covered by lichens and mosses. On recently infected trees the first rings of fructifications usually appear under the lichens, and to a lesser extent the mosses. These statements of observed correlation do not of course constitute proof of a cause-and-effect relation; but, in the opinion of the writer, they strongly suggest an influence.

The size and age of tree seemed, both in general observations and in the permanent sample plots, to be related to the activity of infection, both the amount of necrotic tissue on individual trees and the number of trees killed seeming to vary with size of tree. This is plausible on the grounds that young trees provide less suitable crevices, and support fewer lichens and mosses for harboring the insect and enabling infection, and that potentially more vigorous meristematic tissues are capable of restricting individual infections more successfully and rapidly.

It was decided to test this observation, as well as others with regard to the possible influence of environment on the disease, by including data on these factors with the data gathered from line plots in the survey discussed in Section V.

LINE-PLOT SURVEY

The possible factors examined in the line-plot survey were diameter (d.b.h.) and crown class of the susceptible tree; the stand factors—forest type, percentage of beech in stand, and crown density; the indirect physiographic factors—position on ridge or slope, percentage or angle of slope, aspect (exposure) according to the compass; and the climatic factor—proximity to large bodies of sea water.

Diameter and Crown Class

Size of tree was expressed in this survey in two ways: as diameter (d.b.h., 4.5 feet) and as crown class. When the percentage of beech infected was compared with diameter, no consistent variation in the two was found; the mean percentages of beech infected by *Nectria*, based both on plot-percentage means and on tree totals, for the various four-inch diameter classes were found to range between the narrow limits of 85.0 and 93.5%, and show no correlation with diameter. This result is presumed to signify merely that absolute susceptibility is not influenced by diameter of the trunk. But when the severity of infection of the infected beech (designated by three severity classes: light, medium, and heavy) is compared with diameter, a significant variation is discovered (Table XXI). Examining first the figures for the

TABLE XXI

DISTRIBUTION OF SEVERITY OF INFECTION OF *Nectria*-INFECTED BEECH, BY DIAMETER CLASSES

Region	Diameter by four-inch classes, in.	Number of beech infected by *Nectria*	Per cent of *Nectria* infected beech			Probability of significance of difference in distribution of severity of infection†	
			Light infection	Medium infection	Heavy infection	Between adjacent diameter classes	Between diameter classes 4–7 in. and 12–15 in.
Nova Scotia mainland	4– 7	818	9.4	21.8	68.8	>100 to 1	> 100 to 1
	8–11	368	5.2	13.8	81.0		
	12–15	138	3.6	9.4	87.0	Between 19 and 49 to 1	
	16–19	33*	0.0	15.2	84.8	Between 7 to 3 and 1 to 1	
	20–23	3	(Too few to be significant)				
Cape Breton and New Brunswick	4– 7	1460	27.3	33.3	39.4	>100 to 1	> 100 to 1
	8–11	820	18.8	30.5	50.7		
	12–15	343	23.3	26.0	50.7	Between 9 and 4 to 1	
	16–19	66*	28.8	27.3	43.9	Between 1 to 1 and 3 to 7	
	20–23	8	(Too few to be significant)				

**Probably based on too few trees to be significant.*

†These values are obtained by computing χ^2 according to a method in Fisher (1930: p. 84-85, ex. 11) and converting the value of P, secured by entering the χ^2 table, into probability odds.

areas in the Nova Scotia mainland, it appears that, compared with diameter, the percentage of infected beech with light infection shows a good negative correlation and the percentage with heavy infection a good positive correlation. Since these figures are based on tree totals it is not feasible to compute correlation coefficients; another measure of the reliability of this trend is afforded by computing the significance of the differences between the distributions of the tree percentages (totalling 100%) for the various diameter classes. The table shows that probability odds are low for the significance of such differences as are not in agreement with this trend, and high for all which are in agreement. In the Cape Breton and New Brunswick areas, where the disease has not yet run its full course, this trend is not so clear, but is judged to be definite, none the less. The downward trend of light infection and the upward trend of heavy infection are shown in the graph (Fig. 13). In other words, the amount or severity of infection tends to vary directly with the diameter of the trunk.

With the foregoing relation established, one would expect to find a similar relation between mortality and diameter. The mean percentages of beech dead in the sample plots have been secured on the basis both of tree totals and of plot percentages, and are presented in Table XXII. The actual mean for each sample plot is indicated on the scatter diagrams in Figs. 14 and 15, which show that, although scatter is great, the standard errors (indicated by horizontal lines) are small for the lower diameter classes because of the great numbers of points, and that the class means exhibit a definite tendency for mortality to increase with diameter. This trend has been measured by the correlation coefficient (Table XXII) and found, as expected because of the

TABLE XXII

PERCENTAGE OF BEECH DEAD, COMPARED WITH DIAMETER AT BREAST HEIGHT

Region		Diameter by four-inch classes					Correlation coefficient r	Probability of significance of r
		4–7 in.	8–11 in.	12-15 in.	16-19 in.	20-23 in.		
Nova Scotia mainland	Number of beech	906	405	147	35	4		
	Mean per cent of beech dead, based on tree totals	41.7 ±1.64*	55.1 ±2.47	66.0 ±3.91	60.0 ±8.28	75.0 ±21.65	—	—
	Mean per cent of beech dead, based on plot percentages	41.0 ±2.53	48.3 ±3.73	67.9 ±4.69	62.9 ±12.30	75.0 ±30.96	0.311 ±0.0612	>100 to 1
Cape Breton and New Brunswick	Number of beech	1600	932	372	74	8		
	Mean per cent of beech dead, based on tree totals	17.6 ±0.95	21.4 ±1.34	25.3 ±2.25	31.1 ±5.38	37.5 ±17.12	—	—
	Mean per cent of beech dead, based on plot percentages	16.3 ±1.73	19.6 ±1.99	23.2 ±2.93	28.8 ±5.54	42.9 ±20.20	0.174 ±0.0474	>100 to 1

**The standard error for a mean percentage based on tree totals (such as living and dead) is computed by the formula* $\sigma_Q = \sqrt{\frac{PQ}{n}}$ *where* P *= per cent living,* Q *= per cent dead, and* n *= the total number of trees living and dead.*

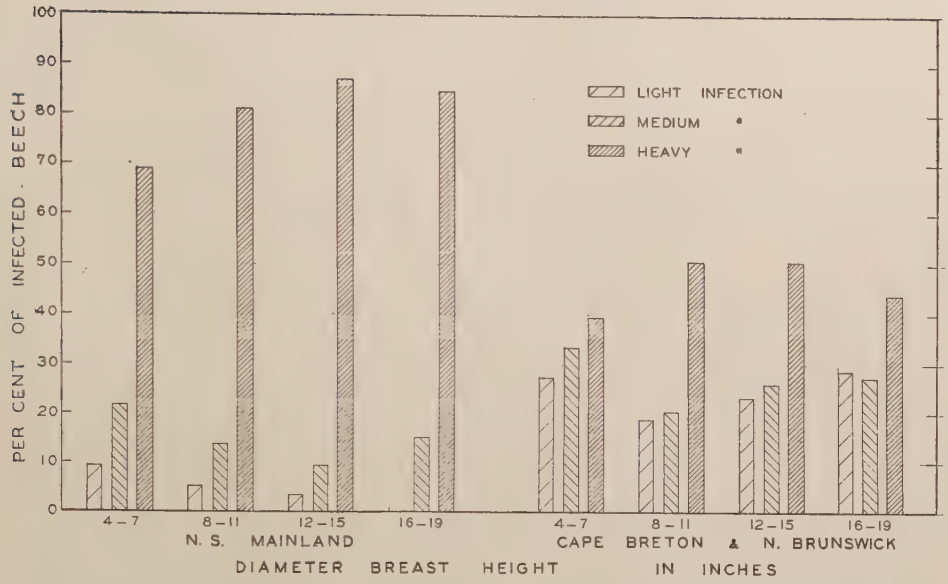

FIG. 13. *Percentages of Nectria-infected beech with light, medium, and heavy infection, by diameter classes; in Nova Scotia mainland, and in New Brunswick and Cape Breton Island.*

scatter, to be small. But the tests of the computed values of r (standard error of r, and probability of significance of the value of r) show that the values secured, though small, are reliable. This in itself does not mean that they

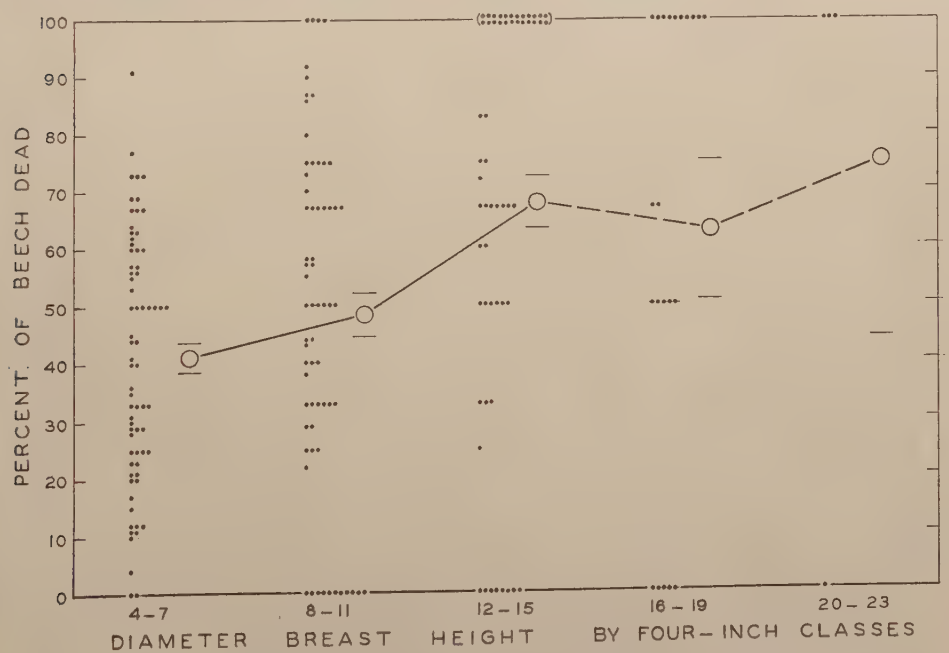

FIG. 14. *Percentage of beech dead (by plots): compared with diameter; for plots in Nova Scotia mainland.*

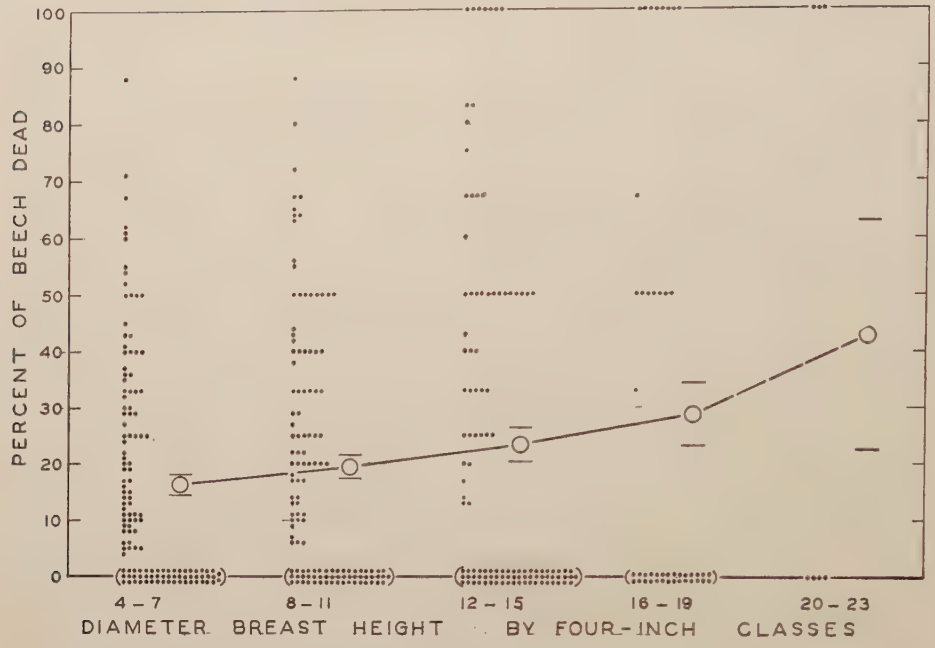

FIG. 15. *Percentage of beech dead (by plots): compared with diameter; for plots in New Brunswick and Cape Breton Island.*

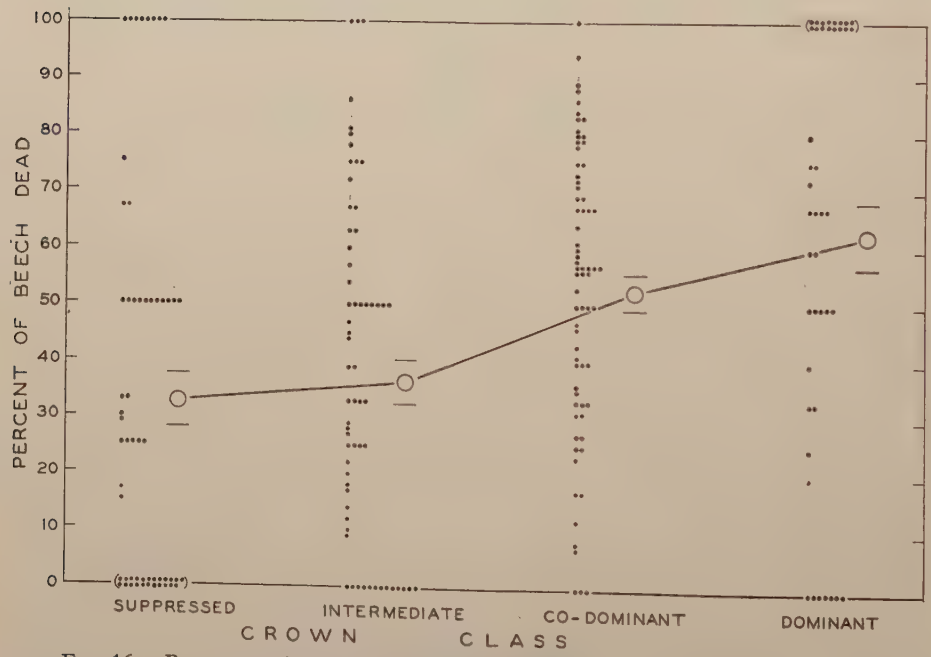

FIG. 16. *Percentage of beech dead (by plots): compared with crown class; for plots in Nova Scotia mainland.*

are significant; the decision as to their significance is largely a matter of judgment. When one considers the innumerable factors (including many of which we are probably not even aware) which must cause local variations both in aggressiveness of the pathogens and resistance of the suscept, the existence of even a small definite tendency for mortality to vary with one of them must be regarded, in the writer's opinion at least, as indication that this factor possibly exerts a definite influence. The question of the nature and biological plausibility of that influence is apart from the foregoing statistical one; it is discussed below.

The other measure of size of the tree employed in this study is crown class. No record was kept of the relation between infection and crown class. The data for mortality have been compiled, as in the case of diameter, on the basis of mean percentages of beech dead according to tree totals and plot percentages, and are presented, with standard errors of the means, in Table XXIII. The scatter of the plot percentages and their means for each crown class are plotted in the scatter diagrams (Figs. 16 and 17), which show, as with diameter, a great scatter, but small standard errors and a definite tendency of the means to vary with crown class. Correlation coefficients computed for the two regions have values of 0.315 for the Nova Scotia mainland and 0.614 for Cape Breton and New Brunswick (as compared with 0.311 and 0.174, respectively, in the case of diameter) and again show satisfactorily small standard errors and high probabilities of reliability. As with diameter, the trend is more pronounced in the case of the Nova Scotia mainland, where

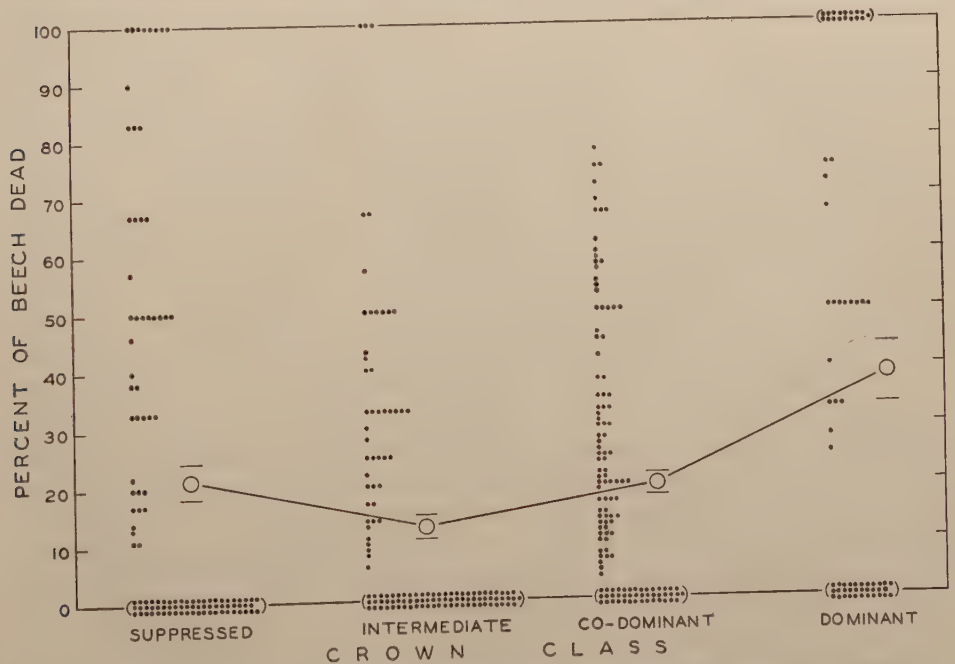

FIG. 17. *Percentage of beech dead (by plots): compared with crown class; for plots in New Brunswick and Cape Breton Island.*

the disease has been active for a relatively long period, than in Cape Breton and New Brunswick.

In short, if one does not object to the reliability of the computed values of r on the ground that the frequency distributions are abnormal, one is faced

TABLE XXIII

PERCENTAGE OF BEECH DEAD, COMPARED WITH CROWN CLASS

Region		Crown classes				Correlation coefficient r	Probability of significance of r
		Suppressed	Intermediate	Co-dominant	Dominant		
Nova Scotia mainland	Number of beech	169	440	772	116		
	Mean per cent of beech dead, based on tree totals	**34.9** ±3.67	**39.6** ±2.33	**54.0** ±1.86	**59.5** ±4.56	—	—
	Mean per cent of beech dead, based on plot percentages	**32.8** ±4.74	**36.6** ±3.92	**52.5** ±3.19	**62.5** ±5.61	**0.315** ±0.05889	>100 to **1**
Cape Breton and New Brunswick	Number of beech	428	703	1714	141		
	Mean per cent of beech dead, based on tree totals	**22.2** ±2.01	**12.4** ±1.24	**21.3** ±0.99	**39.7** ±4.12	—	—
	Mean per cent of beech dead, based on plot percentages	**21.3** ±3.06	**12.9** ±1.95	**20.9** ±2.01	**38.5** ±5.20	**0.164** ±0.04731	>100 to 1

with the question of deciding whether the tendency of *(a)* severity of infection and *(b)* mortality to vary with size of tree is significant biologically. As suggested above, this decision is largely a matter of judgment. The writer believes that plausibility comes to the support of *(a)* the relation between infection and size of tree, in that the nature of the bark has been found in extended observations to vary consistently with size of tree, the larger trees having more sheltering lenticular crevices, mosses, and foliose lichens, all of which favor infestation by *Cryptococcus* and infection by *Nectria* in the ways discussed above. Again, the demonstrated relation between *(b)* mortality and size of tree receives support from the following considerations. Let it be assumed, first, that the heavier attack over a more extensive portion of the bark surface on large trees seems to prevent cambial activity from circumscribing and healing-over individual lesions, as frequently occurs on small trees; instead, the radial growth of countless lesions results rapidly in their coalescence and the death of large areas of trunk surface. Second, since the surface area of the crown increases about as the square of the diameter at breast height, it follows that the conducting tissue of the trunk is more active in larger trees because of the greater demands for sap by the proportionately larger crown; and each unit of the conducting system is more vital to the normal activity of the large tree than of the small one. Further, the larger trees are usually co-dominant or dominant, which means that

their crowns are more exposed and therefore subject to greater water loss by transpiration than small trees, which are usually suppressed or intermediate. It follows from these two points that the destruction of a given proportion of the conducting tissues imposes a more severe toll on the normal metabolism and the life of a large tree with exposed crown than on those of a small suppressed tree with sheltered crown.

Stand Factors

Forest type. Although preliminary observations indicated no obvious relation in the Maritime beech stands between the composition of the stand and the amount of infection or mortality, it was believed that such a relation might well exist and, if it did, would offer a valuable silvicultural weapon in control strategy. For the purposes of the present survey, the stands in which beech is common were divided into four arbitrary forest types: (I) *pure beech*, in which over 70% of the stand are hardwoods and 90% or over of the hardwoods are beech; (II) *beech and tolerant hardwoods*, in which over 70% of the stand are tolerant hardwoods (*Fagus grandifolia*, *Betula lutea*, *Acer saccharum*, and others) and less than 90% of the tolerant hardwoods are beech; (III) *beech, other hardwoods, and conifers*, in which not more than 70% of the stand are hardwoods; and (IV) *beech and conifers*, in which not more than 70% of the stand are hardwoods and 90% or over of the hardwoods are beech. Since the actual survey included only a single plot which fell into Type IV, this plot was grouped with Type III. The mean percentages (based on individual plot percentages) of beech infected in all areas were found to be for Type I, 91.2; for Type II, 89.6; for Type III, 88.7. As was to be expected from the probability values in Table III, the mean percentages of beech infected showed only a slight tendency to vary with forest type. The mean percentages of beech dead in the Nova Scotia mainland plots were found to be for Type I, 48.4; for Type II, 48.9; for Type III, 44.5; similar percentages in Cape Breton and New Brunswick proved to be for Type I, 22.2; for Type II, 18.7; for Type III, 18.5. The mortality data, too, thus show no marked correlation with forest type. The figures as a whole show a very slight trend in favor of a positive relation between the proportion of beech in a type and the amount of disease, and a negative one between conifers in a type and disease; but this trend is so small that no statistical analysis has been made and the relation is assumed to be negligible.

Percentage of beech in stand. A better measure of a possible relation between composition and disease is afforded by a direct comparison of the percentage of beech in the stand with mean percentages of beech infected and dead. The plots have been arranged in 10% classes according to the percentage of beech in stand and the actual class means presented in Table XXIV, together with the mean percentage for the plots in each class of beech infected. Here an irregular but positive trend is observed for the mean percentage of beech infected by *Nectria* to vary with percentage of beech in stand. The scatter diagram prepared from the raw data (Fig. 18) shows that the scatter of individual plot percentages is wide, with resulting rather large standard

TABLE XXIV

PERCENTAGE OF BEECH INFECTED BY *Nectria*, COMPARED WITH PERCENTAGE OF BEECH IN STAND, FOR ALL REGIONS

	Per cent of beech in stand, by 10% classes									Correlation coefficient	Probability of significance of
	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–100	r	
Actual mean of per cent-beech-in-stand class	15.0	24.8	33.7	44.0	54.1	64.2	75.2	84.3	93.6		
Mean per cent of beech (based on plot percentages) infected by *Nectria*	**83.3**	**86.9**	**86.4**	**89.1**	**87.7**	**88.8**	**93.3**	**92.6**	**95.9**	**0.208** ±0.06799	>100 to 1
	±5.76	±3.51	±6.24	±2.21	±2.27	±2.03	±1.44	±1.44	±1.12		

errors for the class means. But the trend is definite and the correlation coefficient, although small (0.208), has a low enough standard error and high enough probability odds of reliability to establish the fact of a small positive correlation between percentage of beech infected and percentage of beech in stand. The mortality figures, similarly compiled, show no tendency towards correlation with percentage of beech in stand and the correlation coefficients are negligibly small and unreliable (for plots in the Nova Scotia mainland, 0.00334 ± 0.1204, with probability of significance odds 1 to 9; for plots in Cape Breton and New Brunswick, 0.0513 ± 0.08781, with probability odds between 1 to 1 and 2 to 3). In short, the data show that the percentage of beech infected by *Nectria* shows a small tendency to vary with percentage of beech in stand, but that this relation is not strong enough to exert an appreciable influence on the percentage of beech killed.

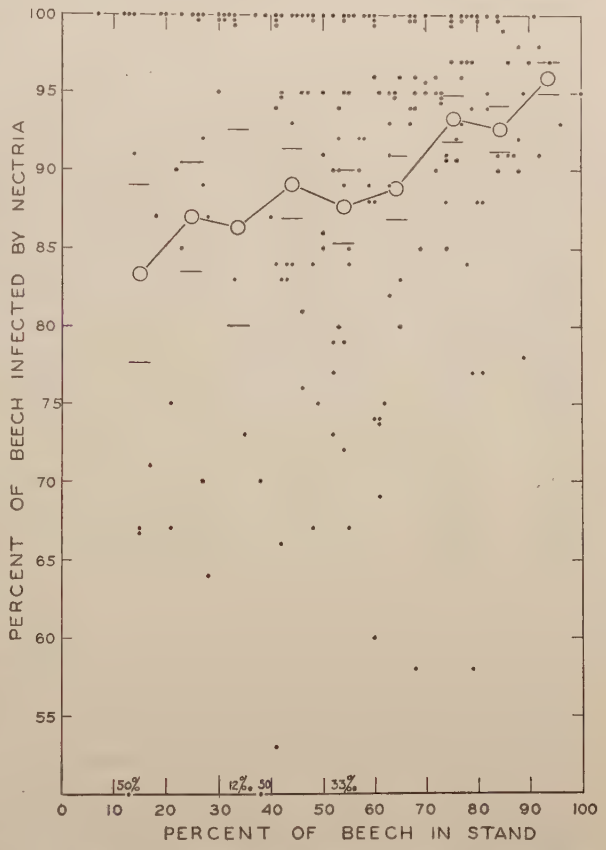

FIG. 18. *Percentage of beech infected by Nectria (by plots): compared with percentage of beech in stand.*

Crown density. Preliminary observations led the writer to believe that stand factors which favor the retention of moisture under the crown canopy promote the activity of the *Nectria* and the virulence of the disease. Among such factors may be included density of the crown canopy and abundance of ground cover and underbrush. Systematic observations on ground cover and underbrush were not made. Notes were recorded in each plot on crown density expressed as tenths, where 0.5 denoted a stand in which 0.5 of the ground was estimated to be shaded and 0.9 denoted approximately 0.9 of the ground shaded, the latter being the greatest crown density which is common in temperate hardwood stands. An important difficulty encountered in estimating crown density, and one which increases with the duration of the disease in a stand, is that the crown density at the time of recording is not the same as it was when the disease began, but decreases progressively; it was therefore necessary to estimate the crown density at the time that the disease

began; it is this figure, designated "past crown density," which is considered here. Computations of mean percentages of beech infected (based on plot percentages) for each past-crown-density class, and dead (based on plot percentages and tree totals), with their standard errors, were made and show that there is no correlation between either percentage of beech infected or percentage dead and crown density. Correlation coefficients were computed for the mortality figures, but proved to be small, less than twice their standard errors, and to have unconvincing probability odds of significance (for the Nova Scotia mainland plots, 0.098 ± 0.1201, with probability odds of significance between 1 to 1 and 2 to 3; for Cape Breton and New Brunswick plots, 0.144 ± 0.0878, with odds between 4 to 1 and 9 to 1).

When severity of infection on the infected beech is compared with crown density, there is seen to be no consistent correlation. In the Nova Scotia mainland the percentage of infected beech with light infection varies directly while the percentage with heavy infection varies inversely with the crown density, a situation the opposite of what was anticipated. In Cape Breton and New Brunswick the situation is more nearly in keeping with expectation, but inconsistent with the Nova Scotia results. The probability odds show that the differences between crown-density distributions of the severity of infection are in nearly all instances greater than can be accounted for by chance. The explanation of these results is not clear; they indicate that some factor or factors other than crown density are operating more effectively.

Indirect Physiographic Factors

Since most of the beech in Nova Scotia and New Brunswick occurs on hardwood ridges, data on three indirect physiographic factors which were thought to have a possible connection with the disease were recorded. These were position of plot on ridge, degree of slope, and aspect.

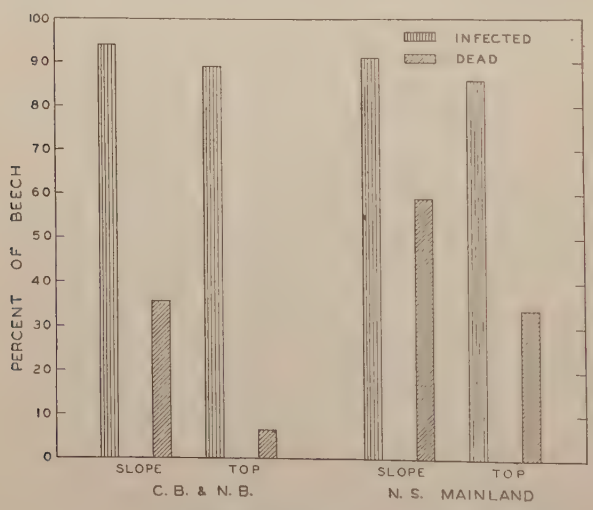

FIG. 19. *Mean percentage of beech infected by Nectria, and dead: compared with position on ridge; for plots in Nova Scotia mainland, and in New Brunswick and Cape Breton Island.*

Position on ridge. It had been noted in preliminary observations that the beech on the slope (or face) of a ridge were killed in greater number than those on the broad top. Since conditions are usually more conducive to drying on the face, owing to greater crown exposure and air currents, it was thought that greater mortality was due less to increased activity of the pathogens than to decreased ability of the tree to withstand an attack of given intensity—for the same reasons discussed under

TABLE XXV

PERCENTAGE OF BEECH INFECTED BY *Nectria*, AND PERCENTAGE DEAD, COMPARED WITH POSITION ON RIDGE

Region		Nova Scotia mainland		Cape Breton and New Brunswick	
Position on ridge		Slope	Top	Slope	Top
Total number of beech		632	438	941	941
Per cent of beech INFECTED, based on	Plot percentages	**90.8**	**85.6**	**94.2**	**88.8**
	Tree totals	**92.1** ±1.07	**87.0** ±1.61	**94.8** ±2.29	**87.4** ±1.08
Difference between slope and top percentages		5.1 ±1.93*		7.4 ±2.53	
Probability of significance of difference†		>100 to 1		>100 to 1	
Mean per cent of beech infected, all regions combined		89.6 ±0.77			
Per cent of beech DEAD, based on	Plot percentages	**59.0**	**35.6**	**34.8**	**6.59**
	Tree totals	**60.9** ±1.94	**34.0** ±2.26	**34.4** ±1.55	**7.01** ±0.83
Difference between slope and top percentages		26.9 ±2.98*		27.4 ±1.76	
Probability of significance of difference†		much >100 to 1		much >100 to 1	
Mean per cent of beech dead, by regions		48.0 ±3.5		19.2 ±1.7	

**The standard error of the difference between two means is computed by the usual formula:* $SE_{m_1-m_2} = \sqrt{SE^2_{m_1} + SE^2_{m_2}}$. *A significant difference between two means should have a standard error of less than one-half of the difference.*

†*These values are odds, and measure the probability that the difference between the contrasted series could not have arisen by chance. They are obtained by computing the constant* χ^2 *according to the formula for "fourfold" tables in Fisher* (1930: *p.* 84) *and converting into probability odds the value of P obtained by entering the* χ^2 *table.*

The odds are found to be more than 100 *to* 1 *that the differences both in mortality and in infection between slopes and tops of ridges are not chance results. In other words, the differences are significant.*

crown class (above). In order to discover whether infection and mortality actually vary with position on ridge, a selection from all the plots was made taking only those which were definitely ridge top and those distinctly ridge slope. The results of this selection and of analysis of the data are presented in Table XXV. It will be observed that, contrary to expectation, there is for both regions a slight but significant difference in the percentage of beech infected, being greater on the slope than on the top. The percentages of beech dead show, as expected, a great difference, as between slope of ridge and top. These differences are shown graphically in Fig. 19. A satisfactory explanation of the infection figures is not at hand, but the writer is confident that the difference in the mortality figures is greater than can be accounted

for on the basis of the infection figures, and believes that the explanation lies in the fact that the crowns on the slope of a ridge are more exposed to drying, and that therefore a given amount of necrotic tissue would exert a more lethal influence on such trees than on ridge-top individuals.

Percentage of slope. Another measure of the same influence was thought to be afforded by steepness of slope. The plots were sorted according to slope and the percentages of beech infected and dead compiled for the different slope classes. The mean percentages of beech infected are exhibited for 10% slope classes (100% slope equalling an angle of 45 degrees) in Table XXVI and show a small and questionable correlation of infection with slope. The mortality data were analyzed similarly and showed for the Nova Scotia mainland plots an r value of 0.192 ± 0.1160, with probability odds between 9 and 19 to 1; the Cape Breton and New Brunswick percentages were so erratic that r was not computed. Thus there is no correlation of mortality with slope. These results suggest that the foregoing explanation of the influence of exposure on death may not be correct—or at least not sufficient.

Aspect. Believing that insolation, prevailing winds, and other factors might exert an influence on the disease, it was decided to compare infection and mortality with aspect (compass direction with the slope faces), since aspect affords a ready index to such factors. The results (Table XXVII) show

TABLE XXVII

PERCENTAGE OF BEECH INFECTED BY *Nectria*, AND PERCENTAGE DEAD, COMPARED WITH ASPECT

Mean per cent of beech (based on plot percentages)	Region	Aspect (described in eight points of the compass)							
		N	NE	E	SE	S	SW	W	NW
Infected by *Nectria*	Nova Scotia, Cape Breton, and New Brunswick	91.1	85.9	85.0	90.0	85.4	88.3	93.8	89.9
Dead	Nova Scotia mainland	47.5	52.4	54.6	43.2	42.6	30.0	45.7	47.0
	Cape Breton and New Brunswick	32.7	14.7	10.8	14.8	24.1	9.7	21.8	19.2

no consistent variation either of infection or of mortality with aspect. The apparently low mortality on the southwest aspect is perhaps explained in part by the fact that only a very few plots had this aspect. It is possible that the southwest aspect is unfavorable to beech; but whether such a condition would increase or decrease resistance to infection is open to question. Little significance can be attached to the greater variability in the Cape Breton and New Brunswick figures, since the disease is still relatively young in these regions.

TABLE XXVI

PERCENTAGE OF BEECH INFECTED BY *Nectria*, COMPARED WITH PERCENTAGE SLOPE OF GROUND, FOR ALL REGIONS

	Per cent slope of ground, in 10% classes*									Correlation coefficient	Probability of significance of
	0–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	90–99	*r*	of *r*
Actual mean of per cent-slope class	2.6	12.4	21.0	30.4	40.0	50.0	60.0	72.5	100.0		
Mean per cent of beech (based on plot percentages) infected by *Nectria*	**87.4** ±1.57	**90.9** ±1.82	**89.2** ±2.62	**90.3** ±1.87	**93.4** ±3.05	**93.9** ±1.65	**90.8** ±6.13	**91.7** ±3.00	**94.2** ±0.91	**0.164** ±0.0693	between 49 and 99 to 1

*100% *slope* = 45° *angle of slope.*

Climate

Proximity to sea water was the only climatic factor examined for its possible influence on infection and mortality. The plots were arranged according to their distance by 10-mile classes from the nearest large body of salt water, and the means, with their standard errors, computed of the plot percentages of beech infected and dead in each 10-mile class. The results as a whole showed no consistent trend and appear inconclusive. In the first two classes (0–9, and 10–19 miles from the sea), however, both infection and mortality figures for the Cape Breton and New Brunswick plots decreased with distance from the sea, while in the Nova Scotia mainland plots both figures increased. Whether this result has significance is not clear. It was thought from preliminary observations that fogs along the coasts, which seem to account in part for the abundance of lichens and mosses in the Maritime forests and to favor the proverbially rapid reproduction of the softwoods, might also stimulate the activity of the *Nectria*. The present comparisons can hardly be regarded as conclusive evidence that no such influence exists; but they indicate that it is not pronounced.

SUMMARY

Preliminary observations and a line-plot survey in Nova Scotia and New Brunswick have shown that while the amount of infection is almost uniformly great in the areas affected, the mortality varies in different localities but is generally related to the duration of the local outbreaks. Furthermore, it has been shown that local variations in both infection and mortality are correlated with certain differences in size of tree, nature of stand, and physiography. Small but definite positive correlations exist between percentage of beech infected by *Nectria*, and percentage of beech in stand, position on slope of ridge, and steepness of slope; further, severity of infection shows definite correlation with diameter (d.b.h.), and questionable correlations with forest type and crown density. Mortality, expressed as percentage of beech (over 3 in. d.b.h.) killed, is correlated definitely with diameter, crown class, and position on slope of ridge; and questionably with forest type, and steepness of slope.

In no case are the correlations high. Although this fact might on first thought tend to weaken one's confidence in the results, the writer believes that the existence of even a small determinable correlation, when statistically reliable, has great meaning because it indicates a trend so strong that it stands out above the many other influences which must be exerted locally both on the pathogens and on the suscept. The mere existence of correlation between two variables is no proof that one causes or even influences the other. But if from other sources one has an understanding of the nature of the relation between two variables which have been found statistically to move together, then correlation coefficients and other statistical devices are useful in affording a reliable estimate or measure of the magnitude of the relation. Since the computed correlations in the foregoing data are in accord with

biological facts or theories, they are judged by the writer to have significance in the present study. The question of their applicability to control practice is apart from the present discussion and will be dealt with below.

IX. Control

The problem of control of the beech bark disease demands consideration from two aspects, *(a)* that of a favorite ornamental shade tree, and *(b)* that of one of the less valuable of the timber producing hardwoods at present. Since fungal infection is dependent on previous attack by the woolly beech scale, direct control of the insect may be regarded as one means of preventing the development of the disease. That direct control of the fungus would be difficult, if possible, is suggested by experience with other fungal bark diseases of trees. Indirect means, because of the necessity for relatively small expenditures, are more favored in forest-disease control than the costly direct means, applicable to ornamental trees. The direct means which are discussed below by reason of their applicability to ornamental beech are (1) exclusion from regions at some distance from infested areas by nursery inspection, and (2) protection or early eradication in exposed or newly infested areas. The possible indirect means which may find employment in forest control are (1) the discovery and cultivation of fungal parasites or insect predators or parasites of *Cryptococcus*, and (2) the practice of silvicultural measures designed to decrease the aggressiveness and virulence of the pathogens. An added economic measure of great importance in severely attacked stands is the timely salvage of the timber that has succumbed.

A. CONTROL ON ORNAMENTAL BEECH

Exclusion

One of the most satisfactory means of controlling a biotic disease is the prevention wherever possible of the distribution into uninfested regions of the pathogens that cause the disease. In the case of the beech bark disease, nursery inspection and prohibition of the transportation of nursery stock or other materials likely to harbor the pathogens would, with a high degree of certainty, prevent the disease from spreading to regions isolated by large natural barriers. The exercise of such measures within a continuous area would at best be of variable worth as a retarding factor, their value depending on the distances involved, the direction of prevailing winds, and the—as yet undetermined—natural distribution of the fungal pathogen. Climate, as a limiting factor of spread, applicable to both beech ornamentals and forests, may be an operating influence of great importance; but on this subject no information has yet been assembled.

Protection and Eradication

The writer has made no experiment on the direct protection from fungal infection of beech exposed to such infection in the regions harboring the fungus, by spraying for the insect; but the protection experiments described in Section VII C, D, indicate that when trees are protected against infestation

or disinfested within a year of attack, fungal infection does not generally follow. Direct control of *Cryptococcus fagi*, by protecting trees exposed to infestation, and eradicating the insect from infested trees by the employment of insecticides, can be readily and effectively practised. The references to this insect in Europe abound with recommendations and instructions for scrubbing and spraying susceptible portions of the tree with all manner of contact insecticides. Complete success is reported to attend their thorough application. The most highly endorsed materials in recent times are a German proprietary insecticide called "carbolineum" and various English mixtures whose active ingredients always include one of the coal tar hydrocarbons.

The writer has investigated the problem particularly with respect to New England conditions, and the results have been satisfactory (Ehrlich, 1932 a). There seems no reason to suppose that the successful measures employed would not be equally effective in other areas. With a view to selecting an easily obtainable and effective insecticide for New England use, preliminary tests were made in the late winter of 1931 with various strengths of commercial Sunoco oil, homemade kerosene-soap emulsion, nicotine sulphate (Black Leaf 40), and lime-sulphur. The tests were made by soaking an infested area of bark with the aid of a hand spray gun and removing samples of the bark at once and at intervals of several days for microscopic examination. The efficacy of the various materials was determined by placing the bark on the stage of a binocular microscope and gently raising individual nymphs from the bark with a needle so as not to injure them while thus forcibly withdrawing their stylets from the bark. They were then rolled over so that their ventral sides were uppermost. Those not killed by the insecticide indicated their vitality by waving the stylets above their bodies. Others, raised slightly, but not sufficiently to cause complete withdrawal of the stylets from the bark, waved their bodies about, pivoted only on the stylets. A sufficient number of nymphs were examined in this way from every bark sample so as to leave no doubt as to the effect of a particular treatment. The results of these preliminary tests indicated that lime-sulphur and nicotine sulphate are not satisfactory materials but that Sunoco oil and kerosene-soap emulsion are suitable.

Later in the spring of 1931, field tests were made with commercial equipment operated by park employees in the Arnold Arboretum, Boston parks, and the Middlesex Fells Reservation, using Sunoco oil, kerosene-soap emulsion, and nicotine sulphate. These applications were repeated in the spring of 1932. The pertinent results of these tests are brought together in Table XXVIII. It was concluded from these results that Sunoco oil, 1 to 15, is the most satisfactory material. The critical factor in these tests seemed to be the ability of the operator to cover the entire surface of the tree with sufficient thoroughness so that the material wet the fluffy canopy protecting the insects and penetrated to their bodies. This was possible only with the oils. A few trees were also scrubbed with each of these materials, using a long pole with a scrub brush screwed to one end. It was found that this method, when used

TABLE XXVIII

FIELD TESTS WITH CONTACT INSECTICIDES FOR CONTROL OF THE BEECH SCALE

Material	Strength	Place	Number of infested trees sprayed	Number of sprayed trees scale-free*		Per cent control	
				1931	1932	1931	1932
Sunoco oil	1 to 15 of water	Arnold Arboretum	15	15	14	100	93
Kerosene-soap emulsion	25%	Willow Pond Road, Boston	18	12	17	67	95
Sunoco oil, soap, and Black Leaf 40	1 to 10 of water ½ pt. per 40 gal.	Middlesex Fells	69	69	69	100	100
Water	50 gal.	Jamaica Pond, Boston	9	0	8	0	89†
Black Leaf 40, and soap	½ pt. 2½ lb.						

**Number of these trees on which no living scale could be found on careful examination of accessible parts with a hand-lens one month after spraying.*
†Sunoco oil applied with this material in 1932.

with Sunoco oil or kerosene-soap emulsion, was much the most thorough. But it is a difficult method and the labor and expense involved make it applicable only in estates where a small number of valued shade trees are to be kept completely free of the scale.

B. CONTROL IN THE FOREST

Fungal and Insect Parasites

A control measure of technical appeal to the investigator but as yet of uncommon employment by the practical entomologist, horticulturist, and forester is the cultivation of natural enemies of the noxious insect. These include fungi and other insects. Neither in the literature nor in the personal observations of the writer has a fungus parasitic on *Cryptococcus fagi* been encountered. Yet it is believed that watchfulness should not be relaxed, because the environmental conditions favorable to the development of this insect are those commonly suited to fungal activity. For this reason a parasitic fungus, once liberated in an infested region, might well thrive and result in a material diminution of the insect.

Parasitic or predacious insects associated with *Cryptococcus fagi* have occasionally been reported in the literature but none were carefully observed or accorded significance. As early as 1849, Baerensprung stated merely that "Zwischen den Larven lebte eine schwefelgelbe, stark behaarte Milbe." In the following year Hardy (1850 : p. 70) noted: "I must also defer to another opportunity an account of a minute mite, as well as a caterpillar, that accompanied, apparently as parasites, the specimens that have given rise to the remarks now offered"; so far as the present writer is aware, another opportunity never came. Newstead (1901 : p. 28-29) observed a lace-wing fly (*Chrysopa* sp.) on beech trunks infested with *C. fagi* but never found the larvae feeding

on the beech scale. Theobald (1905 : p. 137) stated: "So far no parasite of any importance has been found, but some specimens . . . . had quite a number of larval lady-birds among the felted mass of Coccids. They did not appear ravenous, however, and made little headway against the Coccus." Other observers, including Rhumbler (1915) in Germany, Trägårdh (1921) in Sweden, and an anonymous member of the Forestry Commission (1926) in Great Britain, stated definitely that no parasitic or predacious insects had been found. In Nova Scotia, however, Swaine (1930 : p. 45) reported "an unusual abundance of native Coccinelid beetles, which prey on the coccus." The writer made consistent observations in 1930, 1931, and 1932 on the presence of *Chilocorus bivulnerus* Muls. on *Cryptococcus*-infested beech in seven of the permanent sample plots in Nova Scotia, the results of which are summarized in Table XXIX. This coccinelid was commonly observed feeding

TABLE XXIX

PERCENTAGE OF BEECH IN PERMANENT SAMPLE PLOTS HARBORING *Chilocorus bivulnerus* Muls. (1930, 1931, 1932)

Plot	1930				1931				1932			
	Larvae		Adults		Larvae		Adults		Larvae		Adults	
	Few	Many	Few	Many	Few	Many	Few	Many	Few	Many	Few	Many
1	19	3.4	5.4	0.3	6.5	—	8.2	—	1.4	2.0	1.4	—
2	—	—	—	—	1.4	—	6.9	—	0.4	0.4	—	—
3	—	—	—	—	4.1	—	—	—	4.1	—	—	—
4	—	—	14	—	16	—	4.9	—	0.6	—	2.4	—
5	—	—	—	—	—	—	1.8	—	0.8	—	0.8	—
6	—	—	43	5.4	20	—	13	—	11	1.8	1.8	—
7	—	—	25	4.8	12	—	14	—	1.4	2.0	2.7	—

on the woolly beech scale, but was never found in numbers sufficiently large to exert appreciable curtailment on *Cryptococcus* infestation. Many other species of insects and several arachnids were found to be common on the scale-infested trees but none of them were seen feeding on *Cryptococcus*.

Silviculture

Forestry in America is now passing from the juvenile stage of its progress to more stable and permanent silvicultural practices leading towards sustained yield. Although present economic conditions will retard the profitable employment of these practices, they are bound to occupy an increasingly important place in forest management. When disease control in the forest can be effected in conjunction with such methods, control is most likely to be attempted and offers probably the most useful means of combating many widespread diseases. The studies reported above on the beech bark disease indicate that incidence of infection and mortality vary sufficiently with certain regularizable conditions to hold promise of effecting through them a profitable curtailment in the losses resulting from this disease. Percentage

or severity of infection was found to vary with percentage of beech in stand, steepness of slope, position on top or slope of ridge, and d.b.h., and questionably with crown density. Mortality was discovered to be correlated with d.b.h., crown class, and position on top or slope of ridge. These variations suggest two practices which could well be incorporated in silvicultural operations and whose effectiveness should be tested in sample plots under regulation. Greater infection and mortality associated with position of beech on steep slopes of hardwood ridges indicate that beech should be removed from the slopes and favored on the broad tops of hardwood ridges. The correlation with size of tree, percentage of beech in stand, and crown density suggest that thinning operations should be attempted. Such thinning would have three objectives. First, it would be designed to produce many minor crown openings; this condition should result in decreased abundance and severity of attack by the pathogens, and in retarded activity of those already present. Second, it would remove more beech than other species, in order to lower subsequent infection of beech by decreasing the proportion of beech to other species in the stand. Third, it would cull the trees of larger diameter and higher crown class; this would serve *(a)* to remove the more susceptible individuals most likely, in affected regions, to be already infected and dying; *(b)* it would salvage those less likely than the smaller trees to recover from attack by the fungus; *(c)* it would leave a less susceptible stand capable of producing after a period of years a valuable crop of sound timber; and *(d)* it would supply immediate revenue that might more than pay for the cost of the operation.

Salvage

Dying and dead trees, especially those on which large areas of killed bark adhere and form a substratum for a variety of insects and fungi, become rapidly unfit for merchantable timber by decay of the sapwood. Where the bark loosens and scales off, the exposed areas of sapwood dry and split and in wet weather decay both on the surface and along the fissures. These changes begin on many trees a year before complete death, with the result that when such trees finally die their boles are already more or less deteriorated.

In the Maritime areas where the disease is still active and causing the death of many trees, cutting and marketing of the infected, dying, and dead trees is an urgent necessity if there is to be any salvage from the severely attacked stands. In the newly attacked areas of New Brunswick and Maine, the recently infected stands should be cut before the still-sound timber becomes greatly depreciated in value through splitting and decay.

Salvage operations in attacked stands are recommended, not only because of their immediate economic justification, but also because they constitute important sanitary measures. The various secondary insects and fungi which thrive on decaying slash multiply so prolifically that they soon become an increasing danger to the remaining stand, taking advantage of every wound or weakness resulting from unfavorable soil or weather conditions, attacking and depreciating timber which under normal conditions would maintain a thrifty healthy growth.

In short, control of the beech bark disease in forest stands of the affected and exposed regions should look, first, to salvage of the infected, dying, and dead timber for the purposes of securing the greatest possible return on a rapidly depreciating investment and of preventing the development of unsanitary conditions conducive to further deterioration in the remaining stand. Control should look, secondly, to the possibility of combating the insect pathogen with fungal and insect enemies; and, thirdly, to altering the nature of the stand by forest management designed to minimize the activities of the pathogens and at the same time to substitute a younger, less susceptible stand.

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Bibliography

1. Altum, Bernard. *Chermes fagi*, Buchen-Wolllaus. In, Forstzoologie, III, 2te Aufl., pp. 359–360, fig. 51. Julius Springer, Berlin. 1881.
2. American Association of Economic Entomologists. Common names of insects approved for general use by American economic entomologists. J. Econ. Entomol. 23 : 639. 1930.
3. Anon. Diseased beech trees. Gard. Chron. Agr. Gaz. for 1861 : 850. 1861.
4. Anon. A beech blight. Woods and Forests, 1 : 817. 1884.
5. Anon. [The felted beech coccus.] In, International Forestry Congress at Brussels. J. Board Agr. (London), 17 : 643. 1910.

6. Anon. Felted beech coccus *(Cryptococcus fagi)*. In, Unscheduled pests. Board Agr. Fish. (London), Ann. Rept. Intell. Div., Pt. II, Proc. 1909–1910 : 62–65. 1911.
7. Anon. Beukenwolluis *(Cryptococcus fagi*, Dougl.). Tijdschr. over Plantenziekten (Wageningen), 27 : 61–62. 1921.
8. Baerensprung, F. v. *C. fagi*. In, Beobachtungen über einige einheimische Arten aus der Familie der Coccinen. (Schluss). III. *Coccus*. Ztg. Zool. Zootom., Palaeozool. 1 : 174. 1849.
9. Balch, R. E. Beech coccus *(Cryptococcus fagi* Baerensp.). In, Report on forest insects of Nova Scotia in 1931. Prov. Nova Scotia, Rept. Dept. Lands and Forests, 1931 : 50. 1932.
10. Balch, R. E. M. and L. J. Simpson. Forest insects of the season in the Maritimes and Gaspé peninsula. (Abstr.) Sci. Agr. 13 : 407. 1933.
11. Balfour, J. H. Notice of a diseased condition of beeches at Tynninghame, the seat of the Earl of Haddington. Trans. Bot. Soc. Edinburgh, 7 : 267–268. 1863.
12. Barbey, A. *Coccus fagi* Bärensp. In, Traité d'entomologie forestière. Berger-Levrault, Paris, p. 420. 1913.
13. Beattie, R. Kent. Diseases threatening ornamental and forest trees. J. Econ. Entomol. 26 : 621–624. 1933.
14. Berkeley, M. J. and C. E. Broome. *Psilonia nivea*, Fr. In, Notices of British fungi. Ann. Mag. Nat. Hist. (3rd ser.) 3 : 361. 1859.
15. B[erkeley], M. J. Fungi. Gard. Chron. Agr. Gaz. for 1860 : 8. 1860.
16. B[erkeley], M. J. Beech trees. Gard. Chron. Agr. Gaz. for 1865 : 776. 1865.
17. B[erkeley], M. J. [Editorial on dying of beech.] Gard. Chron. Agr. Gaz. for 1867 : 235–236. 1867.
18. Bertelsmann. Etwas über die Buchen-Wollaus. Deut. Forst-Ztg. 28 : 365–369. 1913a.
19. Bertelsmann. Zur. Buchenwollaus. Deut. Forst-Ztg. 28 : 855. 1913b.
20. Boodle, L. A. and W. Dallimore. Report on investigations made regarding "Beech Coccus." *(Cryptococcus fagi* Bärensprung). Roy. Bot. Gard., Kew, Bull. Misc. Inform. 1911 : 332–343. 1911.
21. Boulger, G. T. The felted beech coccus *(Coccus fagi* Bärensp.). Appendix to, The life-history of the beech. Quart. J. Forestry, 1 : 276-279; figs. 30–32. 1907.
22. Boutilier, Peter G. Regarding the beech trouble in Nova Scotia. Letter to R. H. Wetmore, December 31, 1929.
23. Braucher, R. W. An undesirable foreigner on the American continent (Cryptococcus fagi Baerens.). Canad. Entomol. 46 : 14–15. 1914.
24. Brotherston. The beech coccus. Gard. Chron. (3rd ser.) 36 : 58. 1904.
25. C. C. Disease in beeches. North Brit. Agr. J. Hort. 2 : 11. 1850.
26. Carpenter, George H. Woolly scales of the beech. *Cryptococcus fagi*, Bärensp. In, Injurious insects and other animals observed in Ireland during the year 1902. Roy. Dublin Soc. Econ. Proc. 1 : 207. 1903.
27. Cockerell, T. D. A. *Cryptococcus*, Dougl. In, Tables for the determination of the genera of Coccidae. Canad. Entomol. 31 : 279. 1899.
28. Collins, C. W. Parasite introductions for the gipsy moth and some other forest and shade-tree insects. Prov. Seventh National Shade Tree Conf. 1931 : 129–131. (April) 1932.
29. Collins, C. W. The beech scale *(Cryptococcus fagi* Bärenspr.), recently discovered in New England. J. Econ. Entomol. 25 : 144–145. 1932.
30. Cooke, M. C. *Psilonia nivea* Fr. In, Handbook of British fungi. Macmillan and Co., London and New York. Vol. 2 : 624. 1871.
31. Cooke, M. C. [*Volutella nivea* Sacc.]. In, British Hyphomycetes. Grevillea, 17 : 13. 1888.
32. D. in E. Mittel zur Bekämpfung von Wolläusen. Deut. Forst-Ztg. 29 : 715. 1914.
33. De Wildeman, E. and Th. Durand. *Volutella nivea* (Fries) Sacc. In, Prodrome de la flore Belge. Thallophytes. Bruxelles : Alfred Castaigne. III. Fasc. 6, p. 363. 1898.
34. Douglas, J. W. Pseudococcus fagi, Baerensp. In, Note on some British *Coccidae* (No. 5). Entomol. Monthly Mag. 23 : 152–154. 1886.
35. Douglas, J. W. *Cryptococcus*, n.g. In, Notes on some British and exotic *Coccidae* (No. 16). Entomol. Monthly Mag. 26 : 155. 1890.
36. E., J. M. Bleeding beech trees. Gard. Chron. Agr. Gaz. for 1851 : 740–741. 1851.
37. Eckstein. Wieder die Buchen-Wollschildlaus, Cryptococcus fagi. Deut. Forst-Ztg. 35 : 194–195. 1920.

38. Ehrlich, John. [Bark disease of beech.] Prov. Nova Scotia, Rept. Dept. Lands and Forests, 1930 : 36–37. 1931.

39. Ehrlich, John. The occurrence in the United States of Cryptococcus fagi (Baer.) Dougl., the insect factor in a menacing disease of beech. J. Arnold Arboretum, 13 : 75-80. 1932a.

40. Ehrlich, John. [Bark disease of the beech.] In, Forest pathology in Nova Scotia. Prov. Nova Scotia, Rept. Dept. Lands and Forests, 1931. 43–45; figs. 4–6. 1932b.

41. Ehrlich, John. The beech bark disease in Nova Scotia. Prov. Nova Scotia, Rept. Dept. Lands and Forests, 1932 : 39–45. 1933a.

42. Ehrlich, John. *Nectria coccinea* on beech. Phytopathology, 23 : 10. 1933b.

43. Faull, J. H. [Bark disease of beech.] In, Notes on forest diseases in Nova Scotia. Prov. Nova Scotia, Rept. Dept. Lands and Forests, 1929. p. 40. 1930a.

44. Faull, J. H. [Bark disease of beech.] In, Notes on forest diseases in Nova Scotia. J. Arnold Arboretum, 11 : 58. 1930b.

45. Felt, E. P. The beech scale and a fungus. J. Econ. Entomol. 26 : 510. 1933.

46. Fernald, M. E. Genus Cryptococcus Dougl. In, A catalogue of the Coccidae of the world. Mass. (Hatch) Agr. Expt. Sta. Bull. 88 : 120–121. 1903.

47. Foggo, R. G. Remarks on disease on the beech. Trans. Bot. Soc. Edinburgh, 7 : 344–345. 1863.

48. Forestry Commission (England). The felted beech coccus. (*Cryptococcus fagi* Barensp.). Forestry Commission (London), Leaflet 15 : 1–4; 1 fig. 1926.

49. Fries, Elias. Psilonia. In, Systema orbis vegetabilis. Lundae : e Typographia Academica. Pars 1 : 187. 1825.

50. Fries, Elias. *Psilonia* Fries. 1. *P. nivea.* In, Systema mycologicum, sistens fungorum ordines, generum, et species. Gryphiswaldae : subtibus Ernesti Mauritii. 3 : 450–452. 1832.

51. Fries, Elias. *Psilonia nivea* Fr. In, Summa vegetabilium Scandinaviae, Upsaliae : excud. Typograph. Academici. Sectio posterior, p. 495. 1849.

52. Gillanders, A. T. Cryptococcus fagi (Barensprung). In, Forest entomology. Blackwood, Edinburgh and London. pp. 234–238; fig. 221. 1908.

53. Gorham, R. P. Felted beech coccus, *Cryptococcus fagi* Baerensp. In, Insects of the season 1928 in Prince Edward Island. Ontario Dept. Agr., 59th Ann. Rept., Entomol. Soc. Ontario, 1928 : 8. 1929.

54. Gorham, R. P., G. P. Walker and L. J. Simpson. Felted beech coccus (*Cryptococcus fagi* Baernsp.) In, Insects of the season 1928 in New Brunswick. Ontario Dept. Agr., 59th Ann. Rept., Entomol. Soc. Ontario, 1928 : 16. 1929.

55. Graham, A. R. Beech-bark louse, *Cryptococcus fagi* Baerens. Investigations at Kentville, N.S. Dom. Canada Entomol. Branch, MS. Rept. 8 pp. 1926.

56. Green, E. Ernest. *Cryptococcus fagi* Baerensp. In, Observations on British Coccidae in 1914, with descriptions of new species. Entomol. Monthly Mag. 51 : 180–181. 1915.

57. Harbach. Zur Bekämpfung der Buchenrinden-Wollaus. Deut. Forst-Ztg. 29 : 491–492. 1914.

58. Harbach. Die Bekämpfung der Buchenrinden-Wollaus und der Blutlaus. Deut. Forst-Ztg. 42 : 1005. 1927.

59. Hardy, James. Disease in beech trees. North Brit. Agr. J. Hort. 2 : 169–170. 1850.

60. Hardy, James. (No title.) On *Coccus fagi.* In, Report of the meeting of the Berwickshire Naturalists' Club for the year 1883. Berwickshire Naturalists' Club Proc. (in B.N.C. Hist.) 10 : 263. 1885a.

61. Hardy, James. *Coccus fagi* in the Ravensworth Woods. Berwickshire Naturalists' Club Proc. (in B.N.C. Hist.) 10 : 607–608. 1885b.

62. Hartig, Robert. (No title.) Bericht Über die IV. Versamml. Deutscher Forstmänner zu Greifswald 1875 : 94–103. Julius Springer, Berlin. 1876.

63. Hartig, Robert. Die krebsartigen Krankheiten der Rotbuche. Z. Forst-und Jagdwesen, 9 : 377–383. 1878.

64. Hartig, Robert. Die Buchen-Wolllaus, *Chermes fagi* Kltb. In, Untersuchungen aus dem forstbotanischen Institut zu München I. Springer, Berlin. pp. 156–162. Taf. IX. 1880.

65. Hayden, Richard J. A new beech pest. Horticulture (Boston), 10 : 127. 1932.

66. Hewitt, C. Gordon. Note on the occurrence of the felted beech coccus *Cryptococcus fagi* (Baerens.) Dougl. in Nova Scotia. Canad. Entomol. 46 : 15–16. 1914.

67. Hutchings, C. B. The felted beech coccus, *Cryptococcus fagi* Bärensp. In, The shade tree insects of eastern Canada for the year 1925, with remarks on their activities and prevalence. Quebec Soc. Protection of Plants, 18th Ann. Rept. 1925–26 : 116. 1926.

68. Judeich, J. P. and H. Nitsche. Die Buchen-Wollschildlaus, *Coccus (Cryptococcus) fagi* Bärensp. In, Lehrbuch der mitteleuropäischen Forstinsektenkunde III. (8te Aufl. Ratzeburg, J.T.C., Die Waldverderber und ihre Feinde); pp. 1250–1252; fig. 342. Ed. Holzel, Wien. 1895.

69. Kaltenbach, J. H. ? Chermes fagi n. sp. In, Die Pflanzen=Feinde aus der Classe der Insecten. Stuttgart; Jul. Hoffman. III Abt. p. 631. 1872.

70. Kessler. (Einige Beobachtungen an *Chermes fagi* Kaltb.) In, XXXI. Bericht des Vereines für Naturkunde zu Cassel (Kassel) 1883–1884 (Vortrag 13) : 29–30. 1884.

71. Kickx, Jeon. *Psilonia* Fr. (non Cord.). *P. nivea* Fr. In, Flore cryptogamique des Flandres. Gand: Librairie Générale de H. Hoste. Tome 2 : 285. 1867.

72. L., P. (No title.) [Beech bark infested by *Cryptococcus fagi*, Bär.] J. agr. prat. 29 : 202. 1916.

73. Lambotte, E. Psilonia Fr. non Corda. 1. Ps. Nivea. In, Flore Mycologique Belge. Verviers: Impr. G. Nautet-Hans. Tome 3 : 256. 1880.

74. Libert, M. A. *Psilonia nivea* Fr. In, Plantae cryptogamicae quas in Arduenna collegit. Leodii: Typis Jacobi Desoer, Bibliopolae, in Foro Sti.-Lamberti; Fasiculus Quartus: exs. No. 387. 1838.

75. Lindau, G. *Volutella nivea* Sacc.: In, Rabenhorst, L. Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. Fungi imperfecti: Hyphomycetes (2te. Halfte), Leipzig: Verlag von Eduard Kummer; 2te. Aufl. I, 9 : 492. 1909.

76. M., A. Insect on beech. Gard. Chron. Agr. Gaz. for 1870 : 389. 1870.

77. MacDougall, R. Stewart. The beech-felted scale *(Cryptococcus fagi)*. In, Insects of the year 1907. Trans. Highland Agr. Soc. Scotland (5th ser.), 20 : 305–306. 1908.

78. MacGillivray, Alex. D. Cryptococcus Dougl. In, The Coccidae. Scarab Co., Urbana (Illinois); pp. 132, 147. 1921.

79. Marchal, Paul. *Cryptococcus fagi* (Bärensprung) Douglas, p. 263. In, Notes sur les Cochenilles de l'Europe et du nord de l'Afrique. (1re partie). Ann. Soc. Entomol. France, 77 : 223–309; pl. 3. 1908.

80. Massee, George. Volutella nivea Sacc. In, British fungus-flora. George Bell and Sons, London. Vol. 3 : 474. 1893.

81. [M'Intosh, C. Disease in beech trees.] North Brit. Agr. J. Hort. 1 : 409. 1849.

82. [M'Intosh, C. Aphis Fagi.] North Brit. Agr. J. Hort. 2 : 45. 1850.

83. [Motherwell, W. R. Beech bark-louse.] In, Rept. of the Minister of Agr., Dom. Canada for year ended March 31, 1926 : 98. 1926.

84. Munro, J. W. Note on the felted beech coccus. Quart. J. Forestry, 19 : 283–289. 1925.

85. Newstead, R. Felted beech coccus *(Cryptococcus fagi*, Bärensprung). In, The injurious scale insects and mealy bugs of the British Isles. J. Roy. Hort. Soc. 23 : 249–250; fig. 111. 1900.

86. Newstead, R. [References to *Cryptococcus fagi*.] In, Monograph of the Coccidae of the British Isles. Vol. I. Ann. Vol. of the Ray. Soc. for the year 1900 : 1, 4, 28–29, 41; pl. A, fig. 2. 1901.

87. Newstead, R. Genus Cryptococcus (Douglas); and Cryptococcus fagi (Bärensprung). In, Monograph of the Coccidae of the British Isles. Vol. II. Ann. Vol. of the Ray Soc. for the year 1902 : 214–221; pl. 70. 1903.

88. Newstead, R. The felted beech coccus. J. Board Agr. (London), 11 : 755–760. 1905.

89. Nüsslin, Otto. Die Buchen-Wollschildlaus *(Coccus fagi* Bärenspr.). In, Leitfaden der Forstinsektenkunde. Berlin : Paul Parey. p. 433; fig. 3466, 348. 1905.

90. Nüsslin, Otto. Die Buchen-Wollschildlaus *(Coccus* [*Cryptococcus*] *fagi* Bärenspr.). In, Leitfaden der Forstinsektenkunde. Berlin: Paul Parey. 2te. Aufl. p. 98; fig. 63b, 66. 1913.

91. Ormerod, Eleanor A. Beech-bark "felt-scale". *Cryptococcus fagi*, Baerensprung. In, Report of observations of injurious insects and common farm pests during the year 1897. Rept. 21 : 6–10. 1898.

92. Ormerod, Eleanor A. Beech-bark felt-scale. *Cryptococcus fagi*, Baerensprung. In, Report of observations of injurious insects and common farm pests during the year 1899. (2nd ser.) Rept. 23 : 139–141. 1900.

93. P., R. T. Beech insects. Gard. Chron. Agr. Gaz. for 1858 : 71. 1858.

94. PEIRSON, H. B. [The beech scale.] U.S. Dept. Agr., Bur. Entomol. (mimeogr.). Insect Pest Survey Bull. 12 : 29,397. 1932.

95. PEIRSON, H. B. Beech scale *(Cryptococcus fagi* Baer.). U.S. Dept. Agr., Bur. Entomol. (mimeogr.), Insect Pest Survey Bull. 13 : 43. 1933a.

96. PEIRSON, H. B. Regarding beech scale in Maine. Letter to John Ehrlich, January 7, 1933b.

97. RATZEBURG, J. T. C. Gattung *Coccus*. Schildlaus. In, Waldverderber und ihre Feinde. Nicolaische Verlags., Berlin, 6 Aufl., pp. 428–429. 1869.

98. REH, L. *Cryptococcus fagi* Bärenspr., pp. 351–352. In, Zue Naturgeschichte mittel- und nordeuropäischer Schildläuse. Allgem. Z. Entomol. 8 : 351–356. 1903.

99. REH, L. Bekämpfung der Buchenrinden-Wollaus und der Blutlaus. Anzeiger für Schädlingskunde, 3 : 19–21; figs. 1, 2. 1927.

100. REICHLING. Die Buchenwollaus, *Cryptococcus fagi*, Bärenspr., in Westfalen sowie über ihre Bekämpfung. Jahresber. westfal. Provinzialver. Wiss. Kunst. (Muenster) 47–48 : 15–17. 1920.

101. RHUMBLER, L. Zur Biologie der Buchenrinden=Wollaus *(Cryptococcus fagi)*. Deut. Forst-Ztg. 29 : 265–273. 1914a.

102. RHUMBLER, L. Die Buchenrinden-Wollaus *(Cryptococcus fagi)* und ihre Bekämpfung. J. Neumann, Neudamm, n.d. 32 pp. 1914b.

103. RHUMBLER, L. Verfügung des Ministers für Landwirtschaft pp. vom 19 Dezbr. 1913— III.–12102– betr. Buchenwollaus. Jahrb. Schlesischen Forstvereins (Breslau) für 1914 : 189–199. 1915.

104. RHUMBLER, L. In, Nüsslin, Otto and L. Rhumbler, Die Buchen-Wollschildlaus *(Coccus* [*Cryptococcus*] *fagi)* Bärenspr. In, Forstinsektenkunde. Berlin: Paul Parey. 3te. Aufl. pp. 125–139; figs. 78b, 81, 82. 1922.

105. RHUMBLER, L. Ueber das Schicksal der von der Buchenrinden–wollaus *(Cryptococcus fagi* Bsp.) befallenen Buchen. Z. angew. Entomol. 18 : 590–614; 6 fig.; 1 pl. 1931.

106. RICHTER, HARALD. Die wichtigsten holzbewohnenden Nectrien aus der Gruppe der Krebserreger. Z. wiss. Biol., Abt. F, Z. Parasitenkd. 1 : 24–75; figs. 1–11. 1928.

107. SACCARDO, P. A. 14(3236) Volutella nivea (Fries) Sacc. In, Sylloge fungorum, 4 : 685. 1886.

108. SACCARDO, P. A. [*Volutella nivea* (Fr.) Sacc.] In, Sylloge fungorum, 10 : 720. 1892.

109. SACHTLEBEN, H. Die Buchenwollschildlaus *(Cryptococcus fagi* Bärensp.), p. 98. In, Sachtleben, H. and Pape, H. Krankheiten und Beschädigungen der Kulturpflanzen im Jahre 1920. Mitt. biol. Reichsanst. Land. Forstw. (Berlin), 23 : 26–101; 6 maps. 1922.

110. SCHAFFNER, JOHN V., Jr. [The beech scale.] U.S. Dept. Agr., Bur. Entomol. (mimeogr.), Insect Pest Survey Bull. 11 : 215, 471, 676. 1931.

111. S[CHENK], P. J. De Beukenwolluis. Floralia, 45 : 508. 1924.

112. SCHIERBECK, OTTO. [The beech bark louse.] In, The Imperial Economic Conference Report. Halifax. Prov. Nova Scotia, Dept. Lands and Forests, p. 17, 1932.

113. SCHRÖDER, CHR. Die Buchen-Woll-Laus. Illus. Wochenschr. Entomol. 2 : 225–229; 1 fig. 1897.

114. SEAVER, FRED J. Nectriaceae. North American Flora, 3 : 3–30. 1910.

115. SIGNORET, V. Pulvinaria ? fagi Hardy (1864). In, Essai sur les Cochenilles ou gallinsectes (Homoptères–Coccides), 10e partie. Ann. Soc. Entomol. France (5me ser.) 3 : 36 (212). 1873.

116. SIGNORET, V. 21. *Fagi* Bärensprung (Coccus); and 22. *Fagi* Walk. (Coccus). In, Essai sur les Cochenilles ou gallinsectes (Homoptères–Coccides), 18e et dernière partie. Ann. Soc. Entomol. France, (5me ser.) 6 : 615–616 (453–454). 1876.

117. SINZ. Ueber die Buchen-Wollaus. Deut. Forst-Ztg. 28 : 644. 1913.

118. SINZ. Die Buchenwollaus betreffend. Deut. Forst-Ztg. 29 : 192. 1914.

119. SULC, KAREL. Cryptococcus Douglas. *Cryptococcus fagi* Bärensprung. In, Studie o Coccidech. Sitzungsber. der Königl. Böhmischen Ges. der Wissensch. (Math.–naturwissensch. Classe) 1895 : 22–24; pl. 2 (figs. 6–11, 12b). 1896.

120. SWAINE, J. M. [The European beech coccus, *Cryptococcus fagi* Bären.] In, Notes on forest insect conditions in Nova Scotia in 1929. Prov. Nova Scotia, Rept. Dept. Lands and Forests, 1929. 45. 1930.

121. THEOBALD, F. V. The felted beech coccus *(Cryptococcus fagi*, Barensprung), pp. 176–178, pl. 8. In, The animal pests of forest trees. J. South-Eastern Agr. Coll. Wye, Kent, 13 : 154–185. 1904.

122. THEOBALD, F. V. The felted beech coccus *(Cryptococcus fagi*, Barensprung), p. 137, fig. 38. In, Animals injurious to forest trees. *per cit.* 14 : 109–137. 1905.

123. THEOBALD, F. V. Note on the treatment of the felted beech coccus *(Cryptococcus fagi*, Barensprung). [By Harold King.] pp. 127–128, fig. 33. In, Insects injurious to forest trees. *per. cit.* 15 : 126–128. 1906.

124. THEOBALD, F. V. The felted beech coccus *(Cryptococcus fagi*, Barens.), p. 164, pl. 29A. In, Animals injurious to forest trees. *per. cit.* 16 : 161–165. 1907.

125. THEOBALD, F. V. The felted beech coccus *(Cryptococcus fagi*, Barens.), pp. 178–179. In, Animals injurious to forest trees. *per. cit.* 17 : 174–179. 1908.

126. THEOBALD, F. V. The felted beech coccus *(Cryptococcus fagi*, Barens.), p. 172, pl. 34. In, Animals injurious to forest trees. *per. cit.* 18 : 170–172. 1909.

127. THEOBALD, F. V. The felted beech coccus *(Cryptococcus fagi*, Barens.), pp. 218–219, pl. 35. In, Animals injurious to forest trees. *per. cit.* 20 : 209–220. 1911.

128. THEOBALD, F. V. The felted beech coccus *(Cryptococcus fagi*, Barens.), p. 211. In, Forest tree pests. *per. cit.* 21 : 187–211. 1912.

129. THEOBALD, F. V. The felted beech coccus *(Cryptococcus fagi*, Barens.), p. 333. In, Animals injurious to forest trees. *per. cit.* 22 : 308–333. 1913.

130. TRÄGÅRDH, I[var]. Boksköldlusen. (Cryptococcus fagi, Baer.). Statens Skogsförsöksanstalt (Stockholm) Flygblad No. 21, 4 pp., 1 fig. 1921.

131. VAYSSIÈRE, PAUL. Coccides des hêtres *(Fagus)*, pp. 349–352, and p. 365. In, Contribution a l'étude biologique et systematique des *Coccidae*. Ann. des Épiphyties, 12 : 197–382; fig. 1-95, pl. 1–6. 1926.

132. WALKER, FRANCIS. *Coccus fagi*. In, List of the specimens of homopterous insects in the collection of the British Museum. Part IV : 1086. 1852.

133. WARBURTON, CECIL. [Beech coccus.] p. 209. In, Annual report for 1917 of the Zoologist. J. Roy. Agr. Soc. England, 78 : 209–219. 1917.

134. WARBURTON, CECIL. [Beech coccus.] p. 257. In, Annual Report for 1922 of the Zoologist. J. Roy. Agr. Soc. England, 83 : 253–260. 1922.

135. WEBSTER, A. D. The felted beech coccus. *(Cryptococcus fagi.)* Gard. Chron. (3rd ser.) 44 (1137) : 257. 1908.

136. WEESE, JOSEF. [*Psilonia nivea* Fr.] In, Über Volutella, Psilonia, Chaetostroma und Medusula. Mitt. Botan. Inst. Tech. Hochsch. Wien, 8 : 11–12. 1931.

137. WILKS, W. The beech-tree in England. J. Roy. Hort. Soc. 26 : 598–599. 1901–02.

138. WOLLENWEBER, H. W. *Ramularia, Mycosphaerella, Nectria, Calonectria*. Eine morphologisch pathologische Studie zur Abgrenzung von Pilzgruppen mit cylindrischen und sichelförmigen Konidienformen. Phytopathology, 3 : 197–242; pl. 20–22. 1913.

139. WOLLENWEBER, H. W. Pyrenomyceten–Studien. Angew. Botan. 6 : 300–313; pl. 8. 1924.

140. WOLLENWEBER, H. W. Pyrenomyceten–Studien, II. Angew. Botan. 8 : 168–212. pl. 2–5. 1926.

141. WOLLENWEBER, H. W. Hypocreaceae. In, P. Sorauer. Handbuch der Pflanzenkrankheiten, Bd. II (5th ed.). Die pflanzlichen Parasiten. I Teil, pp. 541–574. 1928a.

142. WOLLENWEBER, H. W. Über Fruchtformen der krebserregenden Nectriaceen. Z. wiss. Biol., Abt. F, Z. Parasitenkd. 1 : 138–173; figs. 1–29. 1928b.

143. WOLLENWEBER, H. W. Fusarium–Monographie. Z. wiss. Biol., Abt. F, Z. Parasitenkd. 3 : 269–516. 1931.

Explanation of Plates

PLATE I

Beech ridge in Inverness County, Nova Scotia, affected by the beech bark disease. The trees with light foliage (pale green or yellow) were infected recently, those with dark foliage died during the current growing season, and those with naked crowns died during the previous year.

PLATE II

A. Trunk of ornamental *Fagus sylvatica*, lightly infested with *Cryptococcus fagi;* Boston, Massachusetts. B. Trunk of forest *Fagus grandifolia*, heavily infested with *Cryptococcus fagi;* Inverness County, Nova Scotia. C. Heavy two years' infestation, showing woolly wax secretion of *Cryptococcus fagi* (× $\frac{2}{3}$). D. Heavy three years' infestation, showing woolly wax secretion of *Cryptococcus fagi* (× $\frac{2}{3}$). E. Light two and three years' infestation with *Cryptococcus fagi*, showing aggregation in lenticular crevices and extrusion of "wool" (× 6). F. Same as Figure E (× 33).

PLATE III

A. First indication of infection; circular lesion, showing ring of macroconidial pustules (× 2). B. Detail of macroconidial pustules, showing erumpent spore masses and upturned ruptured phellem (× 15). C. Circular lesion, showing clusters of perithecia occupying former macroconidial pustules (× 2 to 3). D. Clusters of maturing perithecia, still surrounded by upturned phellar margins (× 15). E. Clusters of mature perithecia, raised above bark and crowding on obscured stromata; ascospore masses beginning to plug ostioles (× 15). F. Clusters of perithecia, collapsed following discharge of ascospores (× 15).

PLATE IV

Same as Plate III, Fig. E (× 33).

PLATE V

A. Cracking bark of dying old beech, showing outlines of original circular lesions. B. Early symptoms of infection: coalescing circular lesions slightly depressed by death of tissues, fruiting pustules occupying central portions; and incipient cracking of bark. C. Exposed young tree, showing ruptured, raised, and sunken localized lesions, and remnants of *Cryptococcus* infestation still active. D. Trunk of young exposed beech, showing old circular lesions under dead foliose lichens, now depressed by surrounding cambial activity; showing also *Cryptococcus* colonies on inner edge of tender marginal callus. E. Two to four years' infected young trunk, showing recent, pustulate, circular lesions, and gnarled and pitted surface resulting from old lesions. F. Long infected deeply pitted young trunk, with fresh *Cryptococcus* colonies developing again on callus.

PLATE VI

A, B, C. Surface and progressively deeper plane views of portion of young, infected trunk, showing two cracked and depressed lesions surrounded by callus, and extent of old and advancing necrosis in the wood. D. Area of trunk with bark freshly removed, showing penetration of circular lesion to wood. E. Beech killed by *Nectria*, dead two years, showing cracked and loosening bark with darkened pustulate areas, and split and discolored wood. F. Mixed hardwood stand on broad ridge-top, Annapolis County, Nova Scotia, showing all beech killed; maple and birch in leaf. G. Roadside view of mixed hardwood stand, Cumberland County, Nova Scotia, showing all beech killed; maple only in leaf.

PLATE VII

A. Stylet track of *Cryptococcus fagi* following anticlinal intercellular course part way through sclerenchyma band in bark of *Fagus grandifolia*. B. Transverse section through lenticel, showing *Cryptococcus* nymphs nestling under phellar shelves at margins. C. Style track passing intracellularly through pericycle parenchyma and deflected horizontally (periclinally) at edge of sclerenchyma band. D. Stylet tracks passing intracellularly through pericycle parenchyma, showing thickening of sheath material in cell lumina. E. Stylet track passing straight through pericycle, not deflected by sclerenchyma. F. Suctorial apparatus of *Cryptococcus fagi*, including salivary glands, rostrum, and stylets passing through periderm. G. Stylet track passing through periderm and cortex.

PLATE VIII

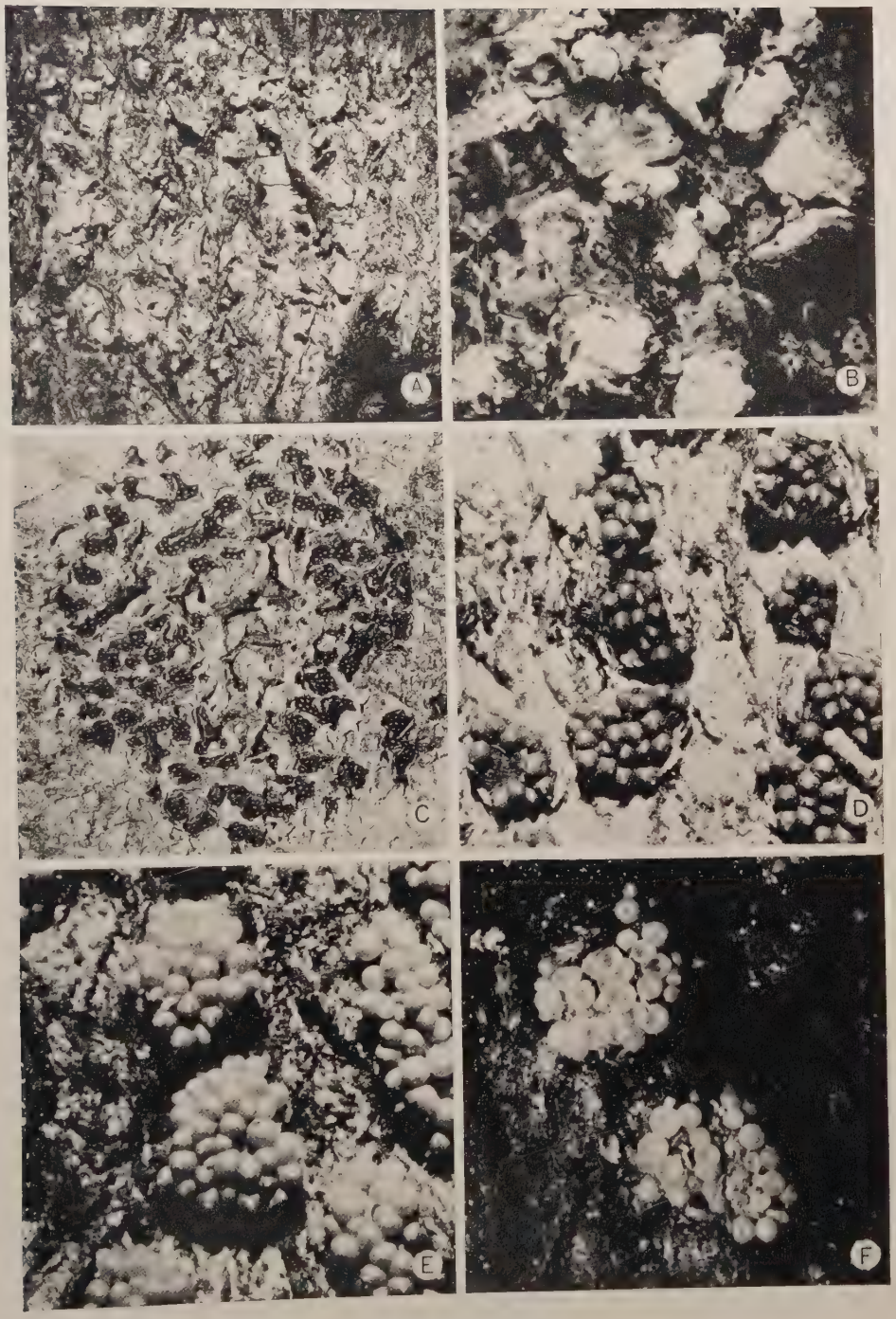
A, B. Young stroma of *Nectria* raising and bursting periderm in bark of *Fagus grandifolia*. C. *Nectria* stroma erumpent in bark, bearing macroconidia *(Cylindrocarpon)*. D. Same as Fig. A. E. Same as Fig. C. F. *Nectria* stroma bearing mature perithecia.

PLATE IX

A. Fresh macroconidial pionnotes of *Nectria* in culture on potato dextrose agar slant (× 6). B. Old dried macroconidial pionnote of *Nectria* in culture on potato dextrose agar slant (× 6). C. Mature *Nectria* perithecia in culture on drying potato agar Petri plate, showing columns of ascospores discharged under moist conditions (× 33). D. Moist chamber tent used for greenhouse inoculations. E. Wood surface of artificially wounded and bark-inoculated beech, showing infected areas. F. Another method of maintaining moisture for greenhouse inoculations of potted sapling beech; absorbent cotton wick carries water from pail to trunk, water seeps down trunk and keeps moist the cotton collars sealing celluloid inoculation chambers. G. Detail of portion of celluloid inoculation chamber, showing bottom sealed by collar of wet absorbent cotton, moist bark within chamber, and signs of successful inoculation. H. Beech trunk, showing method of protecting uninfested and disinfested areas of bark against subsequent attack by wrapping in tarred factory cotton. I. Beech trunk, showing method of protecting uninfested and disinfested areas of bark against subsequent insect attack, but not against fungal inoculation with air-borne spores, by covering with fine mesh phosphor-bronze wire screening raised from the bark and sealed at points of contact with "Tanglefoot." J. Surface of bark with periderm removed on trunk of experimental beech, showing method of examining protected areas and adjacent unprotected areas (above) for symptoms of *Nectria* infection; many lesions in unprotected area; few in protected area.

Beech Bark Disease

BEECH BARK DISEASE



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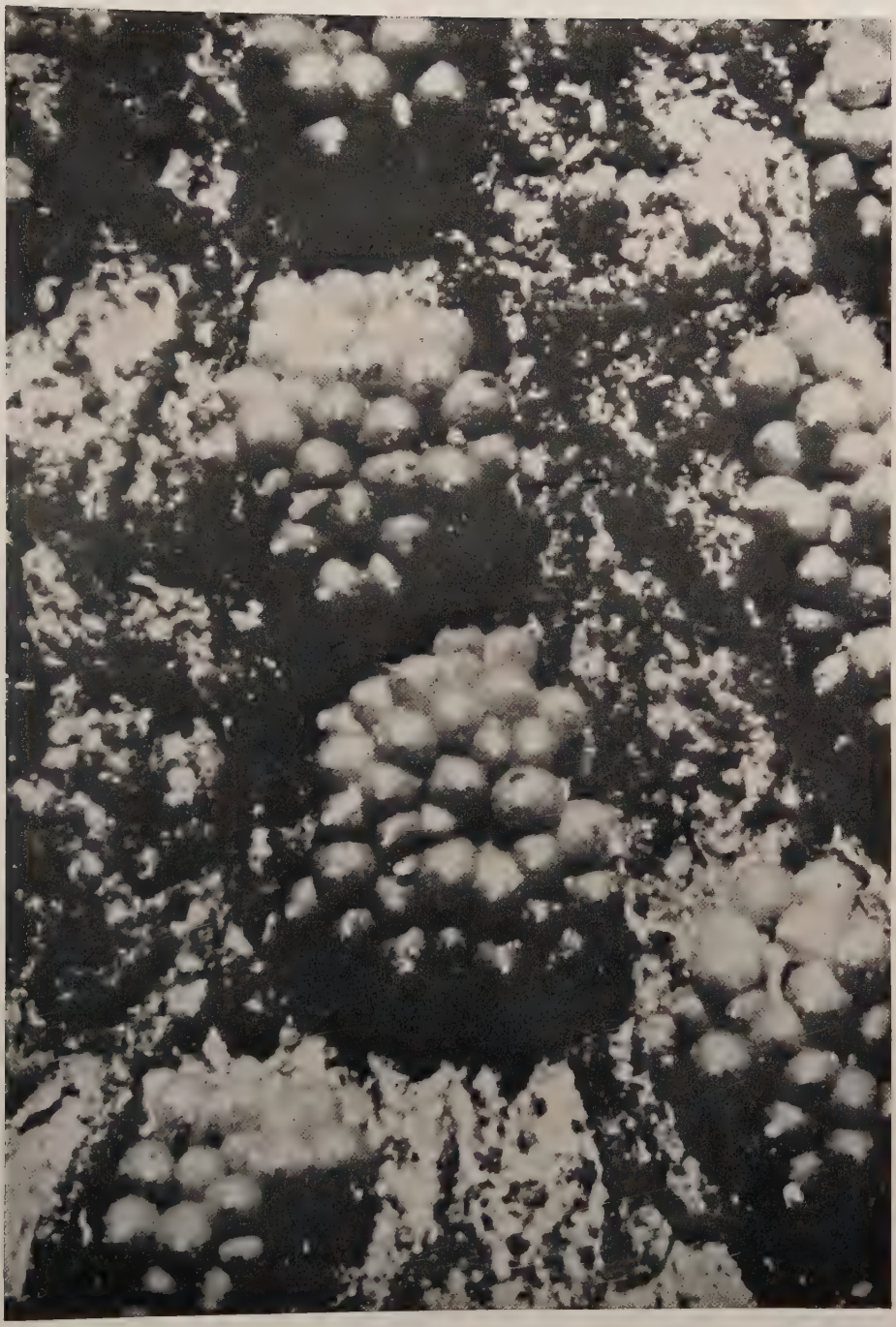

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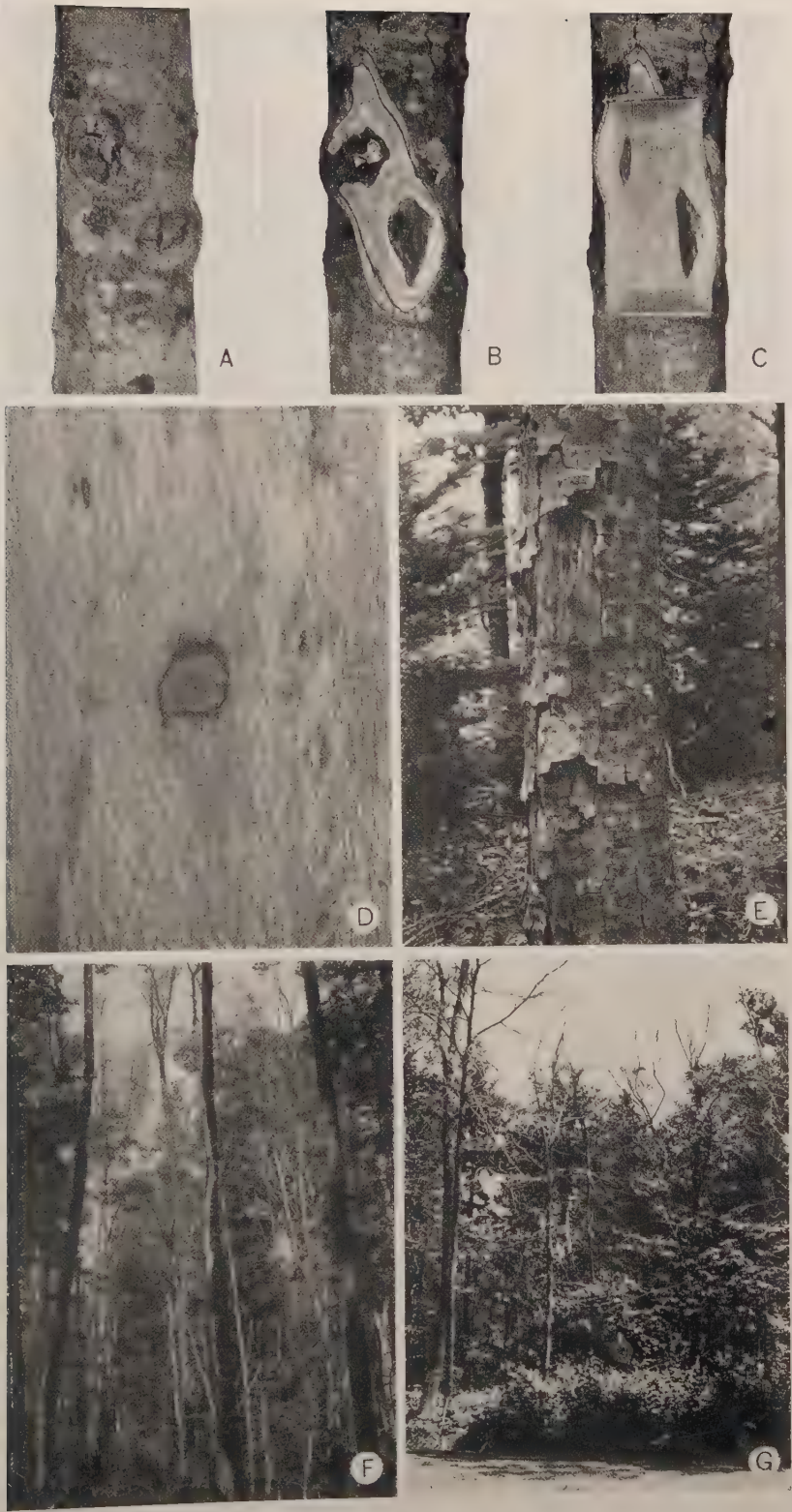

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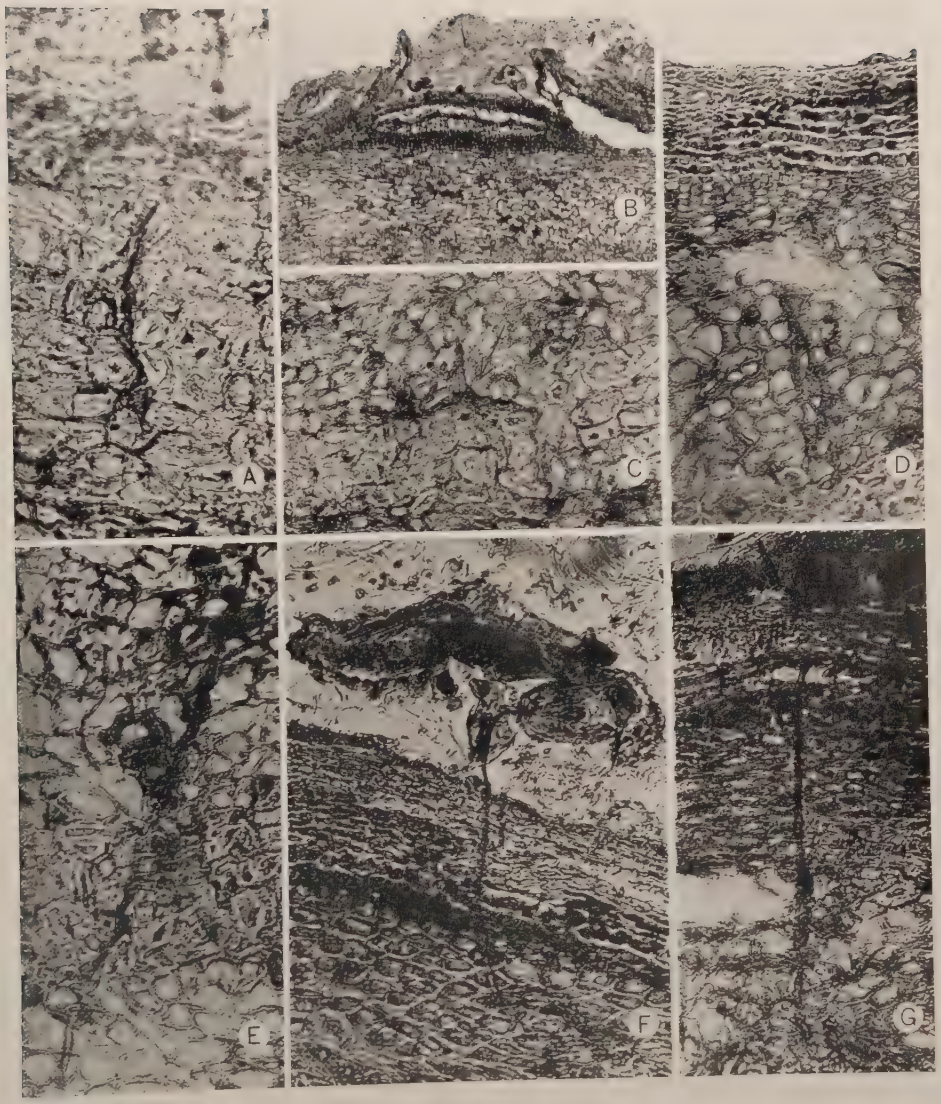

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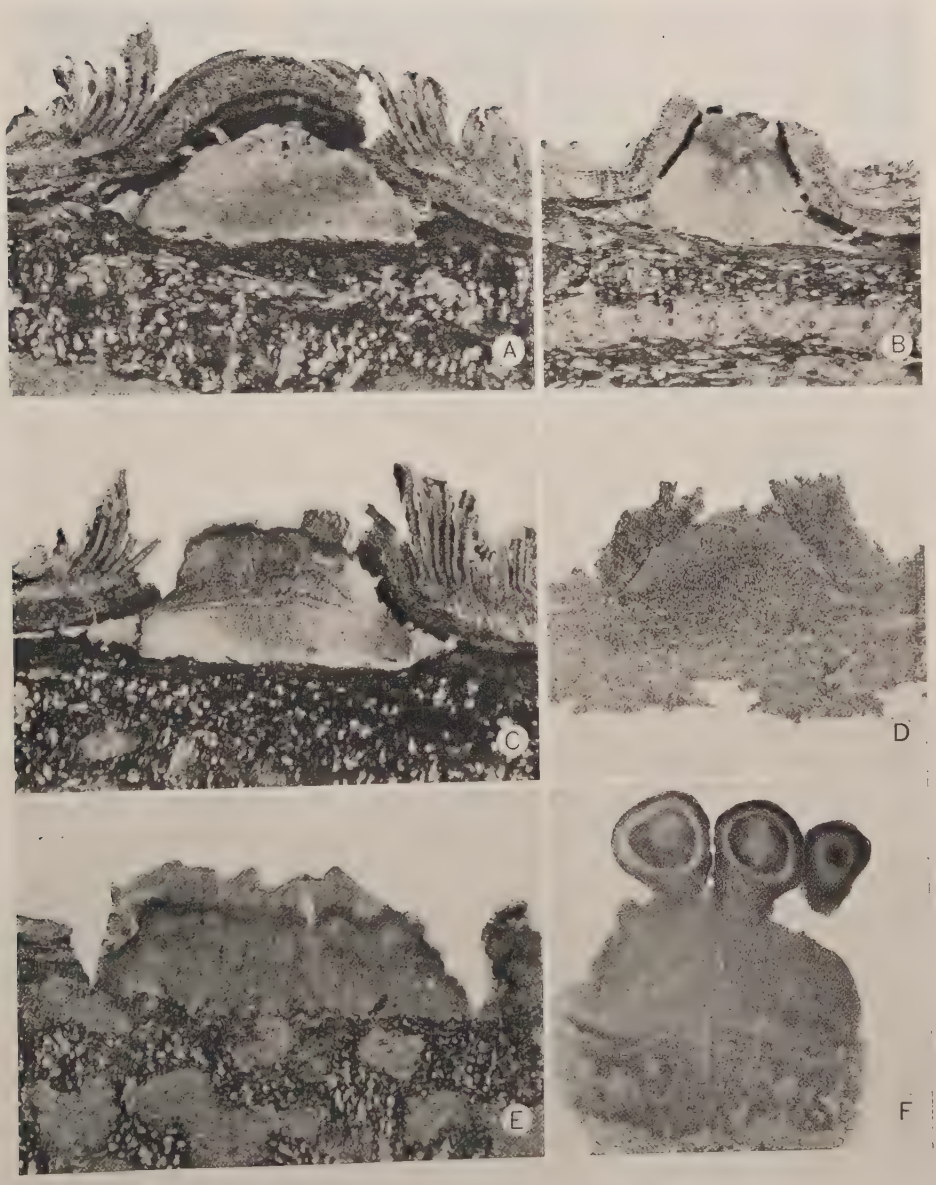

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